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EVALUATION OF NUTRIENT AVAILABILITY IN SOILS,
AND PREDICTION OF YIELD RESPONSE TO FERTILIZATION¹

C. A. Black²

Soil-test values per se are of little value for diagnostic purposes. To provide an appropriate scale of values, the results of laboratory tests must be calibrated in terms of crop responses to fertilization in the field.

Ordinarily, the correlations between laboratory and field results are used in only a qualitative manner. There are at least two reasons why this is the common practice. First, the correlations may not be good enough to justify using them except as a guide. Second, the most suitable application of fertilizer is not always the same for a particular soil-test value. The results of soil tests must thus be "interpreted" in arriving at the recommended fertilizer application. The "interpretation" usually consists of an attempt to take into account the soil-test value and all other factors that may affect the results, without setting down the individual factors in a formal manner and attaching numerical values to the variables.

For situations in which a yield response to application of fertilizer is indicated, the most suitable application of fertilizer can probably never be precisely foretold. The desired objective may nevertheless be approached more closely than is commonly done at present. The more nearly the total problem can be analyzed and formulated into a mathematical operation, the less interpretation will be required, and the more precise will be the predictions.

The objective of the present paper is to outline procedures that will lead to a mathematical formulation of the problem. Essentially, these procedures represent an extension of the ideas described by Bray (2). Although the general procedures are applicable to all nutrients, particular attention will be paid to potassium for illustrative purposes. The present analysis does not deal with the preliminary work of developing soil tests and sorting out the more important fractions of a nutrient present in the soil. Development of soil tests is usually a long process of research involving gradual accumulation of knowledge concerning the behavior of individual nutrients and methods of analysis for different chemical fractions. Techniques for evaluating different fractions have been described by Eid, et al. (3,4) and Pratt (10).

Previous Development

Bray (2) and Arnold and Schmidt (1) have used the Mitscherlich (9) equation with considerable success in the correlation of chemical soil tests with results of field experiments with fertilizers. According to the Mitscherlich hypothesis, the increase in yield resulting from unit increase in supply of a plant nutrient is proportional to the decrement

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from the maximum yield that can be produced as the supply of the nutrient is increased indefinitely. The equation is usually written in the integrated logarithmic form

$$\log (A - y) = \log A - c(x + b) \quad (1)$$

or in the exponential form

$$y = A(1 - 10^{-c(x+b)}) \quad (1a)$$

where y is the yield associated with the effective quantity b of the nutrient present in the soil and seed, plus x units of added nutrient; A is the maximum yield that can be produced as x increases indefinitely; and c is a parameter. The effective quantity b of the nutrient in soil and seed is in the same units as the added nutrient.

When the fertilizer application is zero, the Mitscherlich equation may be written

$$\log (A - y_0) = \log A - cb \quad (2)$$

This is the form in which the equation was used by Bray (2) and Arnold and Schmidt (1). They took the yield with a heavy application of fertilizer as A . The soil test value obtained on a sample of soil from the plowed layer was then assumed to be proportional to b , and was substituted in the equation as b_1 . It was then necessary to use a value proportional to c , called c_1 , so that the product $c_1 b_1$ would be equal to cb .

To estimate the fertilizer requirement, Bray (2) used the following equation:

$$\log (A - y) = \log A - (c_1 b_1 + cx) \quad (3)$$

This equation makes provision for the possibility that the value of c for the added nutrient may be different from the value of c_1 for the nutrient found in the soil by the soil test. If c_1 , b_1 , and c are known for a particular soil, equation 3 may be used to estimate the application of fertilizer required to attain any desired percentage of the maximum yield that lies between the current yield and the maximum.

Nutrient Absorption by Plants in Relation to Analytical Estimation of Nutrient Availability

In the field, the root system of established plants usually extends below the plowed layer into the "subsoil". These "subsoil" roots undoubtedly absorb nutrients if the latter are present in the subsoil. Potassium, for example, occurs in exchangeable form throughout the soil profile. If roots occur in and absorb exchangeable potassium from the subsoil, a part of the potassium available to the plant must be in the subsoil. The exchangeable potassium in the plowed layer thus represents some unknown fraction of the total quantity of exchangeable potassium in the portion of the soil profile occupied by plant roots. Moreover, some of the potassium used by the plants during the season is perhaps present in non-exchangeable forms in the plowed layer and in the subsoil at the beginning of the season. There may thus be two sources of potassium used by plants that are not directly evaluated by the content of exchangeable potassium in the plowed layer of soil. These are the exchangeable potassium in the subsoil and the nonexchangeable potassium in the entire soil.

The fact that the plant absorbs potassium from sources other than the one measured, will result in a low correlation between field and laboratory estimates of availability, where the following two conditions are co-existent: (a) a substantial portion of the potassium used by the plants comes from sources other than exchangeable potassium in the plowed layer; and (b) there is no correlation between the content of exchangeable potassium in the plowed layer and the content of potassium in other forms and locations that affect plant growth. A substantial portion of the potassium used by plants can be safely assumed to come from sources other than the exchangeable potassium in the plowed layer. Thus, it can be concluded that the situation mentioned in (b) did not exist in the work of Bray (2), who obtained relatively good results by considering only the exchangeable potassium in the plowed layer of soil.

The foregoing conclusion is in agreement with present evidence regarding the behavior of soil potassium. The quantity of exchangeable potassium in the subsoil is known to be correlated with that in the surface soil. The rate of release of potassium from nonexchangeable forms is correlated with the initial content of exchangeable potassium. The correlations, however, are by no means perfect. There is thus reason to expect that a closer approximation to the content of available potassium in the soil can be obtained by taking into account the potassium status of the entire root zone. Certain evidence already at hand lends credence to this idea. Unpublished work of Stanford, Dumenil, and Meldrum of the Iowa Agricultural Experiment Station may be cited as an example. These investigators found that for soils having a given content of exchangeable potassium in the plowed layer, the response of alfalfa to potassium fertilization decreased with increasing content of exchangeable potassium in the subsoil. The work of Pratt (10) may be cited in connection with non-exchangeable potassium. He measured the amount of nonexchangeable potassium extracted from a group of soils by a cation exchange resin. He found that the nonexchangeable potassium in this particular form was of significant value in predicting the content of potassium in alfalfa grown on these soils after the correlation of the latter with exchangeable potassium had been taken into account.

It appears, therefore, that because the amounts of the various sources of available potassium in the soil are correlated with the content of exchangeable potassium in the plowed layer, the latter is approximately proportional to the total available potassium in the entire soil. It appears also that the total available potassium might be estimated more precisely than at present by taking into account the possible contributions of all sources of potassium in the entire root zone.

Relating Soil Tests to Plant Measurements of Nutrient Availability

The total available potassium in the root zone is a summation of the amounts of available potassium in each volume unit of soil therein. Where the problem is considered in this light, the modified Mitscherlich equation may be written in the form

$$\log (A - y_0) = \log A - \sum_i (c_{1i}b_{1i} + c_{2i}b_{2i}) \quad (4)$$

where $\sum_i (c_{1i}b_{1i} + c_{2i}b_{2i})$ is equal to cb in equation 2. In equation 4, c_1 and

b_1 are, respectively, the slope constant and the quantity of exchangeable potassium characteristic of each of $i = 1, 2, 3 \dots n$ volume units of soil in the root zone; and c_2 and b_2 are the slope constant and the quantity of potassium in a nonexchangeable form in the same volume units of soil. (The particular form of nonexchangeable potassium should be the one primarily concerned in release of potassium.) This formulation takes into account the possibility that (a) the value of c for exchangeable potassium is different from the value of c for nonexchangeable potassium, and (b) the value of c for each form of potassium depends on the location of the particular volume unit of soil.

Evaluation of $\sum_i (c_{1i}b_{1i} + c_{2i}b_{2i})$ on the volume basis described above is impracticable. The same concepts can be employed on a much simpler basis, however, since in practice only the vertical variation is of particular concern. For purposes of experimental examination, successive horizontal layers of finite thickness, taken from an acre of soil, may be considered as the individual volume units.

For present purposes, it is assumed (a) that yield data are available from a number of field experiments, each with stepwise applications of potassium to describe a response curve up to the point of maximum yield, (b) that the parameters in the Mitscherlich equation have been evaluated for each experiment, (c) that soil samples were taken from each experimental area by depth increments before application of the fertilizer, and (d) that on each soil sample, the content of potassium in the exchangeable form and in the desired nonexchangeable form has been determined in the laboratory.

The problem is then to determine the relationship between values of cb , calculated from equation 2 using the best-fitting values of A and y_0 , and the soil-test values obtained in the laboratory. The technique of linear regression is suitable for the purpose, since cb is linearly related to available potassium. As pointed out above, cb is more properly termed

$\sum_i (c_{1i}b_{1i} + c_{2i}b_{2i})$ when used in the present connection, since more than a single nutrient source and location are under consideration.

The initial equation will have the form

$$\begin{aligned} \sum_i (c_{1i}b_{1i} + c_{2i}b_{2i}) &= c_{11}b_{11} + c_{12}b_{12} + \dots + c_{1n}b_{1n} + c_{21}b_{21} \\ &+ c_{22}b_{22} + \dots + c_{2n}b_{2n} + \text{constant} \end{aligned} \quad (5)$$

where the values of b on the right-hand side of the equality represent measured quantities of potassium in exchangeable form and in the desired nonexchangeable form in the individual soil samples in a particular experiment. The associated values of c are the respective regression coefficients. The second subscript, $1, 2 \dots n$ represents the soil layers numbered from the surface downward. The first subscript denotes either exchangeable potassium (1) or nonexchangeable potassium in the desired form (2).

Equation 5 represents a way of combining in a single expression the quantities of potassium found in different chemical fractions and in different parts of the soil profile. When such an equation has been calculated,

tests of significance of the individual regression coefficients will probably show that most of the independent variables are without significant value in prediction. Such variables can be eliminated and a new equation calculated, employing only the variables of significant value in predicting

$\sum_i (c_{1i}b_{1i} + c_{2i}b_{2i})$. The number of independent variables found to be of significance may be expected to increase with the precision of measurements made on individual experiments and with the number of experiments conducted within the same range of conditions.

The proposed procedure for evaluating various possible sources of a nutrient for plant growth is thus a combination of known techniques. As described for potassium, it provides a way of testing whether the content of exchangeable potassium in the plowed layer of soil provides the best estimate of available potassium in the soil, or whether the estimate can be improved by taking into account additional measures of soil potassium throughout the soil profile.

Estimation of Effect Factor c

The values obtained for the constants in equation 5 will depend to some extent on the value or values employed for the parameter c in the Mitscherlich equation. In practice, therefore, calculation of equation 5 will be delayed, pending investigation of the values of c, to be described in the present section.

The experimental data available for examination are presumed to represent results obtained with a particular crop, kind of fertilizer, and method of application. The parameters A, b, and c in the Mitscherlich equation are presumed to have been evaluated for each experiment by a least-squares method, such as the one described by Eid, *et al.* (4). Under these circumstances, the value of c for the nutrient applied in the fertilizer may decrease with increasing yield level and with increasing fixation of the fertilizer by the soil. To investigate possible variation of c with these causes, the regression of c is computed on the maximum yield A and on the fixation of the fertilizer as found in laboratory experiments employing samples of the surface layer of soil. Both the independent variables are tested at once, since if both are significant the most suitable estimate of c will be obtained when their effects are evaluated jointly. If the effect of fixation is significant, use of the equation for c in subsequent prediction will require data on fixation obtained by the standard procedure on each soil. On the other hand, if neither variable is significant, the average value can justifiably be used. The reason is that if no way can be found to predict c, the average value of c found experimentally will be employed for predicting yield response.

If the regression of c on A, fixation, or both is significant, the value of cb is calculated from equation 2, using the values of A and y_0 obtained by employing the best-fitting value of c for each experiment. The resulting values of cb are then used as the dependent variable for calculating

$\sum_i (c_{1i}b_{1i} + c_{2i}b_{2i})$ in equation 5. If the regression of c on A and fixation is not significant, the values of c for individual experiments are averaged. The best fitting values of A and b for the average value of c are then

calculated for individual experiments. A method for obtaining a least-squares fit on this premise has been described by Eid, *et al.* (4). Finally, the value of cb is calculated for each experiment, and used as the dependent variable for calculating $\sum_i (c_{1i}b_{1i} + c_{2i}b_{2i})$ in equation 5.

Each of the alternative procedures provides three values of y , namely, $y = 0$, $y = y_0$, and $y = A$, from which a value of cb may be found by equation 2. Although the value of c derived from the fertilizer response curve is involved in the process, it is involved only to the extent that it affects the best-fitting values of y_0 and A . This approach is advantageous where the value of c for the added fertilizer differs between experiments, since it avoids biasing the calculated available supply of the nutrient in the soil.

The multiple regression equation relating soil supplies of the nutrient to $\sum_i (c_{1i}b_{1i} + c_{2i}b_{2i})$ is derived on the basis that the various regression coefficients, which together represent the equivalent of c for the soil nutrient, are independent of the soil. The efficiency of the soil supplies of the nutrient may of course vary between experiments, even in the absence of measurable differences in the amounts of the nutrient present. The value of c for the soil nutrient may be expected to decrease with increasing yield level. Although the technique for obtaining $\sum_i (c_{1i}b_{1i} + c_{2i}b_{2i})$ provides no separate estimate of c , possible variation of c for the soil nutrient may be investigated by determining the regression of $cb / \sum_i (c_{1i}b_{1i} + c_{2i}b_{2i})$ on y_0 . If no regression is found, no correction need be made. If a regression is found, however, the best estimate of cb will be obtained by multiplying $\sum_i (c_{1i}b_{1i} + c_{2i}b_{2i})$ by the regression.

Prediction of Yield Response

The next step is the estimation of probable response to fertilization on fields where no experiments have been conducted. Soil samples are taken from these fields in the same depth increments used in the experiments and to the maximum depth found to be of significant value in prediction. The analyses found to be of significant value in prediction are then performed on appropriate individual samples in the same manner used in the experimental work. These data can then be substituted into equation 5 to obtain a value for $\sum_i (c_{1i}b_{1i} + c_{2i}b_{2i})$. If a regression of $cb / \sum_i (c_{1i}b_{1i} + c_{2i}b_{2i})$ on y_0 has been found, the necessary correction is applied to provide the best estimate of cb .

To find the value of A , the estimated value of cb is substituted in equation 2. The average yield produced on the soil in the past is substituted in the same equation as y_0 . The value of A found from solution of this equation and the value obtained for fixation of the fertilizer are then substituted in the regression equation developed to obtain the best estimate of c . (If neither of these factors has been found to be of value in predicting c , this step is omitted, and the average value of c found experimentally is used instead).

The information now at hand includes the best estimates of cb , c , and A for the particular soil. The Mitscherlich equation in the form

$$y = A(1 - 10^{-cx - cb}) \quad (6)$$

may thus be employed to estimate the yield y associated with any desired rate of fertilizer application x .

The final step is to estimate the most suitable rate of fertilizer application. For the condition of unlimited capital, the most suitable rate will be that required to return the maximum net profit. The quantity of fertilizer required to produce the maximum net profit is given by the equation

$$x_p = \frac{\log \left[\frac{2.3cA(M - C_3)}{C_2} \right] - cb}{c} \quad (7)$$

where x_p is the number of units of fertilizer having the cost C_2 per unit, M is the crop value per yield unit, C_3 is the production cost per yield unit, and the other symbols have the same meaning as before. If the supply of capital is limited, the most suitable rate of application will be smaller, and must be computed for the particular conditions of the case concerned. For any rate of application, the value of the net profit P is given by the equation.

$$P = A(M - C_3)(1 - 10^{-cx - cb}) - (C_1 + C_2X) \quad (8)$$

where C_1 is the constant cost per unit of land area, and the other symbols have the same meaning as before.

Other Evaluation Techniques

In the preceding discussion, attention was confined to use of the Mitscherlich equation for estimating nutrient availability in soils. The Mitscherlich equation has been used more extensively than any other equation for describing yield response to fertilizer application. As far as is known, it is as nearly satisfactory as any equation proposed for the purpose. In the eventuality that some other equation is found to be more suitable, however, it will be profitable to introduce appropriate modifications in the approach described in the present paper to adapt the general principles involved to the new equation.

Types of plant response other than yield of dry matter may be used to evaluate nutrient availability in soils. Mitscherlich (8), Mitchell (6), and Mitchell and Chandler (7) have used the Mitscherlich equation to describe the change in percentage content of nutrients in plants with rate of application to the soil. The latter investigators used the equation for evaluation of nutrient availability in soils.

Fried and Dean (5) have applied the isotope-dilution technique to the estimation of nutrient availability in soils. Unfortunately, this technique is not of general applicability in studies of potassium availability because of the short half-life of the potassium isotope. The possible use of a stable element chemically similar to potassium as a suitable tracer is now being investigated by Fried and Dean. If the similarity in behavior is sufficient, the isotope-dilution technique may be employed in field experimental work with potassium.

Another plant-response measurement of nutrient availability in soils can be derived from the change in total absorption of the nutrient with change in rate of application. Mitscherlich (8) has applied his equation

to this relationship as well as to yield vs. rate of application and nutrient percentage vs. rate of application curves. The effect factor c for total nutrient absorption is considerably smaller than that for yield. In fact, de Wit (11) and Dean* have noted that over a considerable range the total nutrient absorption is essentially a linear function of the rate of application. Examination of data in the literature indicates that in many cases the linear relationship holds for rates of application up to those necessary to produce the maximum yield. Dean* has suggested the use of this linear relationship to estimate nutrient availability in soils.

All the plant-composition methods described above except the one employing radioactive potassium can be used in connection with the procedure described in the preceding sections. The necessary basic information is supplied by the same experimental design used in connection with the yield-response method, plus data on the potassium content of the plants.

The regression of $\hat{\sum}_i (c_{1i}b_{1i} + c_{2i}b_{2i})'$ found in this way on the various potassium fractions in the individual soil layers is determined as before. (The prime indicates that the values found in this way are analogous to those described in equations 4 and 5 except that they are based on plant composition data.) To couple results obtained from plant composition measurements to those obtained from yield measurements for use in prediction, the regression of $\hat{\sum}_i (c_{1i}b_{1i} + c_{2i}b_{2i})$ on $\hat{\sum}_i (c_{1i}b_{1i} + c_{2i}b_{2i})'$ is computed. Such use of plant composition data as the basis for predicting yield response to fertilization thus involves a rather more circuitous route of getting to the same point arrived at by the yield-response method described in the preceding sections.

Although it may appear at first thought that a plant composition method could offer no improvement in prediction of yield response when used as indicated in the preceding paragraph, such is not necessarily the case. It is theoretically possible that a plant-composition method will provide the basis for a better prediction of yield response than the yield-response method itself. Whether or not this is the case can be tested in the following way: (1). The yield response to one or more rates of fertilization observed in the experiments is predicted from the soil-analysis data using the procedure described in the preceding section. (2). The soil analysis data are used to predict $\hat{\sum}_i (c_{1i}b_{1i} + c_{2i}b_{2i})'$ and, indirectly, $\hat{\sum}_i (c_{1i}b_{1i} + c_{2i}b_{2i})$ by the plant-composition method, as described above. The yield response is then predicted for the same rates of fertilization as in (1). (3). The information obtained in both (1) and (2) permits partitioning the variance of the observed yield response to fertilization into two parts, namely, that attributable to regression and that not attributable to regression. The total variance is identical in the two cases. The procedure in which the greater proportion of the variance is attributable to the regression is evidently the one that gives the better prediction of yield.

*Dean, L.A. 1953. Yield-of-phosphorus curves. Research Report 272 (mimeo.). Division of Soil and Plant Relationships, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Service, U.S. Dept. of Agriculture, Beltsville, Maryland.

Limitations

The proposed procedure has been presented in terms of the nutrient potassium and certain fractions of that nutrient in the soil. The technique is general, however, and its use is not restricted to the particular conditions described. For example, the procedure provides for the evaluation of any desired number of potassium fractions and depth increments. Moreover, the procedure can be applied to nutrients other than potassium, where appropriate soil analysis and response data are available.

Implicit in the procedure for estimating nutrient availability from the soil-analysis data are the assumptions that with a given quantity of the nutrient in each fraction and in each depth increment, (a) the relative effectiveness of the various forms is constant in all soils, and (b) the total effectiveness changes with depth in the same manner in all soils. No claim is made that either of these assumptions is valid.

As regards assumption (a), present evidence indicates that the availability of a given content of exchangeable potassium may differ between soils. With further research, a new method of analysis may be developed to replace that for exchangeable potassium, or a method may be developed that will permit applying a correction to values of exchangeable potassium before calculation of the multiple regression equation. If such developments are successful, they will reduce the experimental error inherent in the present approach. In the absence of such improvements, the best solution is that of soil stratification, to be described below.

Assumption (b) may readily be perceived to be unjustified in many cases. For example, the depth of root penetration may differ between permeable soils on the one hand and claypan soils on the other. The plants would be expected to absorb relatively little of a nutrient below the upper limit of the claypan on the claypan soils, but they might absorb a considerable amount below that depth on the permeable soils. Such differences would lead to increased experimental error in the analysis and to poorer predictions for both types of soils.

Two different methods might be employed to minimize such difficulties. First, for purposes of statistical analysis, the quantity of the nutrient below the depth of root penetration could be considered to be zero. With this modification, differences in root penetration between experiments could be present without introducing unnecessary experimental error. If it were found from the results of such an analysis that the content of one or more fractions of the nutrient below the depth of root penetration in certain soils was of significant value in prediction (the significance would be derived from the data on the soils having deep root penetration), proper use of the regression equation in subsequent prediction would require knowledge of the nature of the particular soil to which the application was to be made.

Second, the soils could be stratified according to their properties, and enough experiments conducted on each group to permit stratification in making the analysis of the data. In practice, this procedure will undoubtedly be more successful than the procedure described in the preceding paragraph. Soil stratification permits partial elimination of unmeasured and unknown variables that affect the relationship being investigated. Application of the stratification procedure is limited by the prac-

tical consideration of the number of experiments that can be conducted.

The existence of unmeasured and unknown variables that differ between soils will no doubt limit the geographical applicability of the results obtained by the procedure described. Thus, although the procedure permits a more comprehensive accounting for factors that may affect the results, its success in prediction still depends on relative constancy of the assemblage of unmeasured conditions that may affect the relationships obtained empirically. The relationships will differ between years with constant locations. The relationship finally used for prediction should therefore be derived from several years' results. The relationships will differ between locations because of both soil and climatic effects. How widely a given set of coefficients can be applied without exceeding specified limits of precision cannot be predicted.

Present evidence suggests that there may be some difference between crops with respect to the regression coefficients for the different fractions of the nutrient in the soil and for the same forms at different depths. In addition, the effect factor c may vary between crops. There is thus need for an evaluation of the relationships for each crop. As a first approximation, differences between varieties can probably be neglected. The most important differences between varieties from the present standpoint is probably their relative yield. Yield differences are taken care of automatically in the proposed procedure.

The proposed procedure has fewer limitations than others that have been described for the purpose. In the present stage of development, therefore, existence of the limitations pointed out above does not constitute an argument against the use of the procedure. Rather, the limitations represent obstacles to be surmounted by further investigation.

SUMMARY

A procedure is described for evaluating nutrient availability in soils and for estimating yield response to fertilization. The procedure consists of the following steps:

1. A series of uniform field experiments is conducted, in each of which the curve of yield response to different rates of fertilization is determined. Using this information, the availability of the nutrient in the soil is expressed in terms of cb in the Mitscherlich equation.

2. Laboratory data on the content of the nutrient in one or more chemical fractions are obtained by analyzing soil samples taken by fixed depth increments from the individual experimental areas.

3. The dependence of cb on the content of the nutrient in each chemical fraction and at each depth for all experiments is expressed in a single multiple regression equation. The significance of each independent variable is tested, and only those variables of significant value in predicting cb are retained in the final equation.

4. The relationship developed in (3) is used in connection with the Mitscherlich equation to predict probable response to fertilization from soil analysis data obtained on samples from areas not included in the experimental development. If the experimental data demonstrate its value, an auxiliary equation for estimating the value of c for the fertilizer is used to improve the prediction of yield response.

The possible use of expressions other than the Mitscherlich equation for describing the yield response is pointed out. The manner in which plant-composition techniques for evaluating nutrient availability can be used in connection with the general procedure is described. Certain limitations inherent in the procedure are noted.

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EFFECTS OF ORGANIC MERCURY COMPOUNDS ON
ENZYMATIC OXIDATION OF MALIC ACID¹

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Ethylmercuric chloride was one of several organic fungicides which Walker (19) found would inhibit the respiration of *Myrothecium verrucaria* mycelium. Similar organic mercurials are known to inhibit a number of sulfhydryl-containing respiratory enzymes (1,2). It seemed desirable, therefore, to compare the action of the fungicides, ethylmercuric chloride (EMC) and phenylmercuric chloride (PMC), with that of the standard sulfhydryl enzyme inhibitor, *p*-chloromercuribenzoic acid (CMBA), on respiratory enzymes from *M. verrucaria*. A preliminary survey of the soluble dehydrogenases in a mycelial extract showed malic dehydrogenase to be the most active, so it was chosen for the present study.

METHODS

Mycelial pellets of *M. verrucaria* (strain QM460) were grown by the technic of Walker (19) which was based on that of Darby and Goddard (5). They were harvested and washed by suction filtration and blended for 1 minute in a Waring Blendor in 0.01 M pH 8 PO₄ or "tris" (trishydroxymethylaminomethane) buffer to give a mycelial suspension of about 100 mg dry weight per 10 ml. This suspension could be stored in the refrigerator for about 4 days without significant loss of enzyme activity.

Enzyme preparations were made by centrifuging 10 ml of the suspension to remove most of the liquid and grinding the mycelium in an ice bath in a Potter-Elvehjem homogenizer containing 0.5 ml of 0.01 M pH 7 buffer and 2 g. of 100-mesh pyrex glass. The homogenate was then diluted to 10 ml with buffer and centrifuged at low speed to remove the glass and cellular debris. Finally, the suspension was centrifuged at 20,000 times gravity to separate the soluble supernatant and particle fractions. The former contained more than 80 per cent of the total activity and was used for most of the work reported.

Enzyme activity was determined at 30°C, principally by a colorimetric technic (16) in which malic oxidation was coupled through DPN (diphosphopyridine nucleotide (Schwartz)) and diaphorase to an indophenol dye (sodium 2,6-dichlorobenzenoneindo-3-chlorophenol). The diaphorase was an abbreviated Straub-type heart muscle preparation described by Throneberry (14,16). The organic mercurials were dissolved in 0.2 N KOH to facilitate solution, adjusted to pH 8, and diluted to 0.001 M stock solutions.

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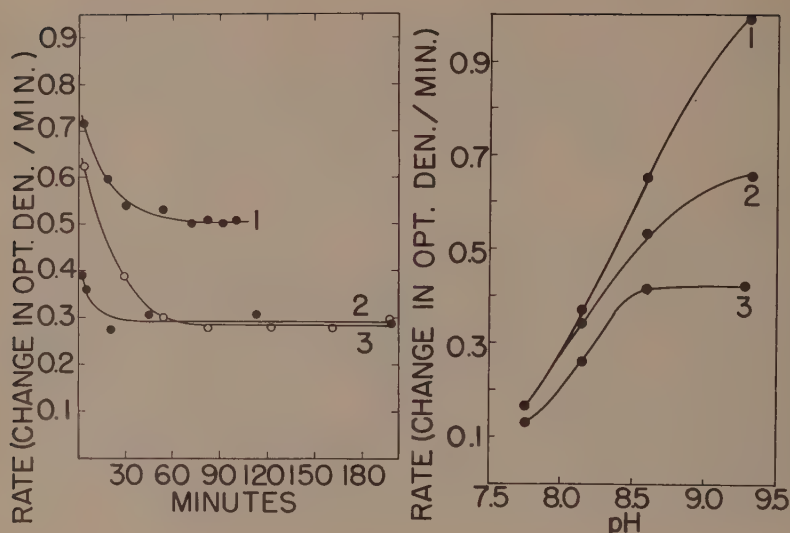


Fig. 1. (left) Malic dehydrogenase inactivation in storage at 30°C.

Fig. 2. (right) Effect of pH and DPN on malic oxidation. Curve 1, 2, and 3 are for 4, 2, and 1 mg DPN, respectively.

The added potassium salt was shown not to affect the results. The optimum conditions established in this work and order of addition used were as follows: (1) 0.5 ml 0.2 M pH 8 phosphate or "tris" buffer, (2) 0.2 ml 0.1 M pH 8 malate, (3) 0.3 ml of 10 mg/ml pH 8 DPN, (4) 0.3 ml diaphorase (volume depending on the preparation), (5) 0.3 ml 4.5×10^{-4} M dye, (6) water to 2.4 ml total volume, (7) mercurial solution, and (8) enzyme solution to give maximum rates up to 0.6. Rates were calculated as change in optical density per minute from colorimeter readings taken at 5 second intervals for 1 to 2 minutes. Cyanide was not used to bind oxalacetate as is frequently done (6) because it inhibited the system (ca. 25 per cent) even at 10^{-4} M. However, oxalacetate accumulation was apparently not sufficient to affect the reaction under the conditions described, since the rates remained constant throughout the experimental period. Furthermore, oxalacetate itself caused no significant dye reduction with this enzyme preparation.

RESULTS

Although the enzyme solution was fairly stable at 0°C, it lost 25 to 50 per cent of its activity rapidly at 30°C. This drop occurred so quickly that it was not possible to measure enzyme activity immediately after raising the temperature to 30°C. After one hour incubation at 30°C, however, the remaining fraction was stable for several hours (Fig. 1) and this treatment was used routinely. The incubated enzyme preparations

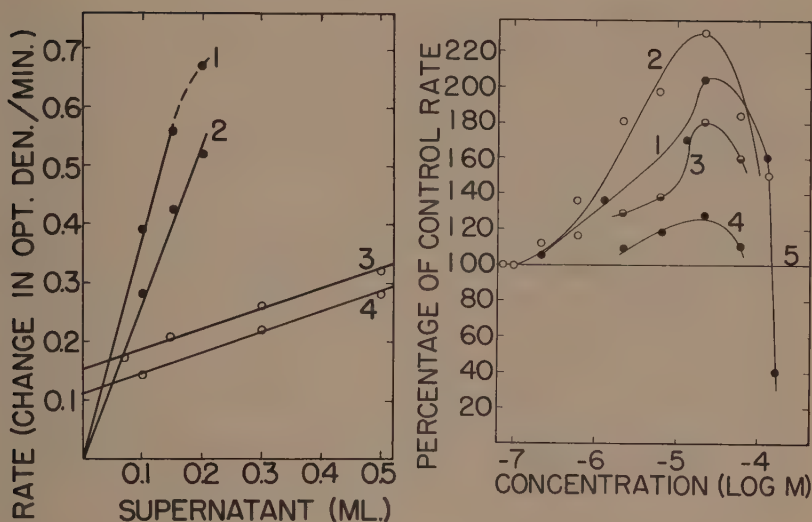


Fig. 3 (left). Proportionality of rate to enzyme concentration. Diaphorase used for curves 3 and 4 contained some malic dehydrogenase activity.

Fig. 4 (right). Effect of ethylmercuric chloride on reaction rates for 4 different supernatants.

showed lag periods in the colorimetric assay of as much as 40 to 60 seconds. These did not appear in spectrophotometric measurements of DPN reduction so it was apparent that diaphorase or dye was involved as well as aging of the enzyme. Although the reason for this effect is not known, it did not interfere with colorimetric assay of dehydrogenase activity when rates were measured after the lag period. A similar lag period was observed with aged malic dehydrogenase preparations from corn germ (16).

Figure 2 shows the general effect of pH and DPN concentration on enzyme activity. Because of increasing autooxidation of the reduced dye at higher pH values, no true pH optimum was established and pH 8 was chosen for the routine assay conditions. It is evident that the DPN requirement of the system was strongly dependent on pH and was unusually high. TPN (triphosphopyridine nucleotide) did not replace DPN with this malic dehydrogenase. Under the conditions described the rates were found to be proportional to enzyme concentration up to rates of 0.4 to 0.6 (Fig. 3).

The effect of the mercurials on the dye reduction system varied with concentration. When added to the enzyme in low concentrations (ca. 10^{-7} to 10^{-5} M) just before the reaction, the 3 organic mercurials caused a stimulation with the maximum rate lasting from 30 to 40 seconds. With EMC (Fig. 4) the optimum concentration was about 4×10^{-5} M and the stimulation, as percentage of control, varied from 20 to 130. Similar results were observed with PMC and CMBA, but the optimum concentra-

tions were lower and more variable. At mercurial concentrations above the optimum, the duration of the stimulation decreased and at 4×10^{-5} to 10^{-4} M inhibition occurred at the start of the reaction. With HgCl_2 no stimulation was observed and inhibition began at about the same concentration as with the organic mercurials. Because of solubility limitations, changes in inhibition with time, and variability in response among enzyme preparations, no precise comparison of the inhibitive action among the four compounds was undertaken. However, the representative data in Table 1 show no striking differences among the compounds. The extent of inhibition increased with time of exposure of the enzyme to the inhibitors before the reaction was started, as shown in Fig. 5 for CMBA. PMC and EMC gave similar responses, but HgCl_2 exerted its maximum inhibitive effect almost immediately. Incubation of diaphorase with EMC before the reaction also showed increasing effect with time while a similar treatment of DPN had no effect. These observations indicate that the mercurials acted both on the dehydrogenase and the diaphorase.

Table 1. Inhibition of dye reduction by the 4 mercurial compounds added immediately before the reaction as percentage of control rates

HgCl_2	M	4×10^{-6}	8×10^{-5}	2×10^{-4}
	per cent	94	72	50
EMC	M			3.2×10^{-4}
	per cent			45
PMC	M		8×10^{-5}	1.2×10^{-4}
	per cent		76	26
CMBA	M		8×10^{-5}	1.2×10^{-4}
	per cent		80	58
				2×10^{-4}
				10

Increasing the DPN concentration caused a decrease in the extent of inhibition by the organic mercurials. With CMBA, some experiments showed typical competitive interaction with DPN (Fig. 6) while others indicated a more complex interaction, suggesting a mixture of competitive and noncompetitive action. EMC and PMC plots were of the latter type. A similar study of malate and CMBA interaction showed no competitive relationship.

In attempting to explain the stimulatory effect of low concentrations of the organic mercurials on the dye reduction system, the following possibilities were considered. First, the dehydrogenase preparation, or the diaphorase preparation, contained an oxidase capable of reoxidizing the reduced dye (11, 12, 13) which was more sensitive to the mercurials than the dye reduction system (A, Fig. 7). Second, the dye reduction system contained a source of peroxide which, with the peroxidase known to be present in the dehydrogenase preparation, would reoxidize reduced dye (B, Fig. 7). In this case, either the peroxide-forming system or the

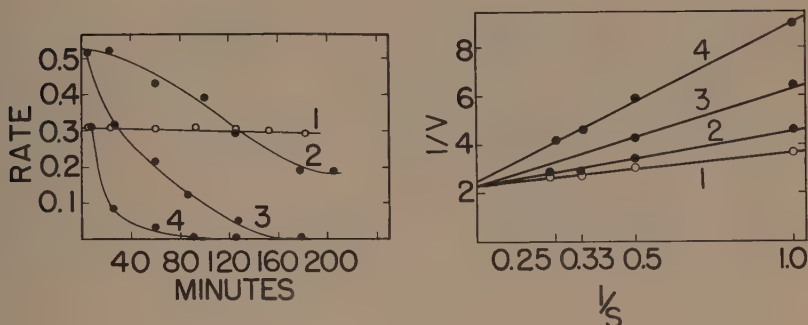


Fig. 5 (left). Change in rate after incubating the supernatant with *p*-chloromercuribenzoic acid. Curve 1, control; curve 2, 4×10^{-6} M; curve 3, 4×10^{-5} M; curve 4, 1×10^{-4} M.

Fig. 6 (right). Competitive inhibition test for DPN and *p*-chloromercuribenzoic acid. Curve 1, control; curve 2, 8×10^{-5} M; curve 3, 12×10^{-5} M; curve 4, 16×10^{-5} M.

peroxidase would have to be more sensitive to mercurials than the dye reduction system. Third, the complete system provided an alternate electron acceptor mechanism competing with dye reduction which was more sensitive to the mercurials than the latter (C, Fig. 7).

The first of these possibilities was eliminated by showing that there was no oxidation of reduced dye in the presence of enzyme and diaphorase. The second possibility was tested by adding catalase to the complete dye reduction system to prevent peroxidation of reduced dye. Catalase treatment did increase the rate of dye reduction, indicating some peroxide formation, but the effect appeared to be too small to account for the mercurial stimulation observed. However, this possibility cannot be considered as eliminated altogether. The third possibility was tested, first, by showing that the stimulation effect was a property of the pig heart diaphorase rather than the dehydrogenase part of the dye reduction system. Reaction mixtures consisting of chemically reduced DPN (DPNH) (7), diaphorase, mercurial, and dye showed greater stimulation than the complete system. Furthermore, the mercurials caused no stimulation of DPN reduction measured spectrophotometrically in a system consisting only of malate, enzyme, and DPN. Because other pig heart diaphorase preparations were found to be appreciably autoxidizable (8) it seemed possible that electron transport to oxygen might be competing with dye reduction. Attempts to show that dye reduction in the complete system was more rapid in the absence of oxygen were inconclusive. Rates were not consistently higher under anaerobic conditions, and only in one experiment did they approach those involving mercurial stimulation under aerobic conditions. A more direct test of diaphorase autoxidation by spectrophotometric measurement of DPNH oxidation gave rates too slow to account for the stimulation effect. It seems unlikely, therefore, that the stimulation effect was due to a mercurial-sensitive alternate electron

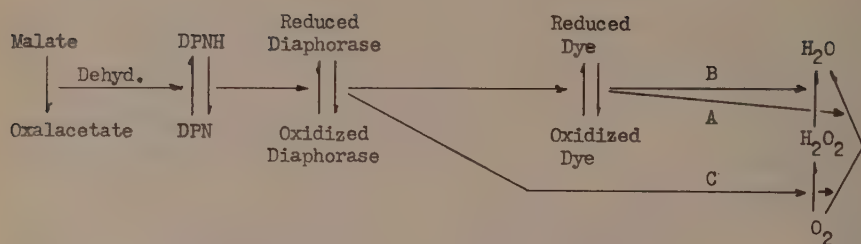


Fig. 7

pathway to oxygen. It must be concluded at present that subinhibitory levels of the organic mercurials had some temporary effect on the diaphorase which increased its ability to reduce the dye.

DISCUSSION

The properties of the *M. verrucaria* malic dehydrogenase in the dye reduction assay system showed some differences from those of the malic enzyme from other sources. Both the DPN requirement and the optimum pH appeared to be unusually high. The marked effect of pH on the DPN requirement also appears to be a new observation for this type of enzyme. The full significance of these observations can be established only by more extensive study, particularly by spectrophotometric measurements of DPN reduction in which the diaphorase-dye step is eliminated.

The action of mercurials on the fungus enzyme system was generally similar to that on soluble malic dehydrogenase preparations from pigeon heart (1). This would indicate that the fungus enzyme also contained essential sulphhydryl groups. However, reversal of inhibition by cysteine or glutathione could not be tested in the dye system because of rapid reduction of the dye by sulphhydryl compounds. No previous report has been found of increasing mercurial inhibition of malic dehydrogenase with time, but inhibition by these compounds of nonsulphhydryl enzymes (2, 4, 10) may indicate that other groups on the enzyme are slowly attacked. The protective action of DPN against mercurial inhibition also appears to be a new observation for the malic system, though similar effects on other sulphhydryl dehydrogenases have been reported (3, 9, 15, 17). The present study indicated that the mercurials acted on both the dehydrogenase and diaphorase parts of the dye reduction system, but there is insufficient evidence at present to determine which is the more sensitive. Vernon, Mahler, and Sarkar (18) have also found that their pig heart diaphorase preparation was sensitive to CMBA.

The temporary stimulation of dye reduction was apparently due to mercurial action on the diaphorase, but it could not be attributed to inhibition of an alternate electron acceptor system. No previous reports of stimulation effects of organic mercurials on oxidative enzyme systems have been found.

The similar effect of all 3 organic mercurials on the malic oxidation system of the fungus indicates that mercurial fungicides like EMC and PMC probably act like the enzyme inhibitor, CMBA, by inhibiting sulfhydryl enzyme systems. Walker (19) found that respiration of intact mycelium of *M. verrucaria* was inhibited 50 per cent after one hour by 2×10^{-5} M EMC. The malic enzyme system was inhibited to the same extent by about $4-8 \times 10^{-5}$ M EMC. It seems likely, therefore, that inhibition of dehydrogenase systems may be involved in respiratory inhibition by the organic mercurial fungicides. Further work is necessary, however, to establish this mechanism and to determine to what extent it is responsible for fungicide action.

SUMMARY

A method is described for the extraction and colorimetric assay of malic dehydrogenase from *Myrothecium verrucaria* mycelium and for studying the action of organic mercurials on the malic oxidation system. Both the DPN requirement and optimum pH were unusually high and the DPN requirement was markedly affected by the pH. The mercurials inhibited both the dehydrogenase and the diaphorase and the effect increased with time. Mercurial inhibition was antagonized by DPN, in part competitively. At subinhibitory levels the organic mercurials caused a temporary stimulation of dye reduction which appeared to be action on the diaphorase. The fungal malic dehydrogenase evidently contained essential sulfhydryl groups, and it seems likely that inhibition of dehydrogenase systems is involved in respiratory inhibition and possibly fungicidal action by organic mercurials.

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FUNGUS LEAF SPOTS OF BROME GRASS IN IOWA¹

Lois H. Tiffany

The grasses in general have been receiving increasing attention as farm crops in recent years. As the use of a specific grass in an area increases, diseases become a more prominent actual or potential factor in production, but frequently there is enough genetic variability within a species to permit the selection of disease resistant lines. A necessary preliminary to such a selection program is a knowledge of the diseases that are present in a particular area and of the causal agents. In Iowa smooth brome (Bromus inermis Leyss) is the most widely planted of the grasses of the present time. During the past two years the fungus leaf spots of brome grass in this area have been observed in the field and the causal organisms isolated and observed in the laboratory. Certain of these fungi are being studied more intensively, but the initial observations are summarized in the following individual discussions.

Pyrenophora bromi (Died.) Drechsler (Helminthosporium bromi Died.)

Drechsler, C. Some graminicolous species of Helminthosporium I. Jour. Agr. Res. 24:641-739. 1923.

Lesions are dark brown or black with a yellowish halo (Fig. 1), limited somewhat by the large leaf veins; at first minute, later elongating and through coalescence may cover most of the leaf surface. Finally the leaf becomes yellow, withers, and dies. The disease occurs throughout the season, becoming widespread very early in the season.

The conidiophores form sparsely on lesions and withered leaves, and are 100-150 by 7-10 microns, rarely 250 microns long, two to six septate, with geniculations not pronounced. Conidia are cylindrical, light brown, one to ten septate, 45-265 by 14-26 microns with the basal cell hemiellipsoidal in shape (Fig. 3). The hilum of the conidium is an inconspicuous scar included entirely in the contour of the peripheral wall. Germination may occur from any cell, but usually from no more than two.

Perithecia may form on diseased leaves as early as July. They are dark brown, subglobose, 0.3 to 0.4 mm in diameter with an irregular ostiolar beak (Fig. 2). A variable number of septate, sterile setae occur near the tip of the beak. Asci develop the following spring in February or March, completing formation in April (Figs. 4, 5). Asci are 170-215 by 40-50 microns in size, enlarging to 300 by 65 microns by discharge time. Ascospores are distichously arranged, light brown, 45-77 by 20-30 microns, three septate, and longitudinal septa are sometimes present in middle segments.

Cultures of H. bromi grew relatively slowly on the several media used. In eight to ten days, black bodies appeared in the agar. The cultures were uniform in appearance, forming first a white fuzzy mycelial growth

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which became gray with age. No conidia were observed in these cultures. One set of isolations from a collection of diseased material near Ames yielded a different type of colony. These cultures were composed of a dark olive green, subsurface mycelium which produced conidiophores and conidia profusely at the surface of the agar. In eight to ten days black subsurface perithecial initials were produced just as they were in the common typical cultures. Asci and ascospores were produced when perithecial initials of both the common and conidial producing cultures were kept at a low temperature (5-10°C) for three months. Both culture types were pathogenic in greenhouse inoculation tests.

Rhynchosporium secalis (Oud.) Davis

Caldwell, R. M. Rhynchosporium scald of barley, rye, and other grasses. Jour. Agr. Res. 55:175-198. 1937.

Lesions are at first dark bluish gray and water soaked in appearance (Fig. 6). Later the collapsed tissue becomes light gray with a dark brown margin. The lesions are frequently elongate, sometimes pointed and variable in size. Under severe conditions, entire leaves may be involved. As is true of many of the leaf spots, it is most severe in the spring and autumn.

Mycelial growth is sparse in the interior of the leaf, remaining principally in a subcuticular position. Superficial stroma which are several cells thick are regularly formed. The conidiophores have been most frequently described as short and rather difficult to observe. Conidia are hyaline, allantoid with a short oblique apical beak, medianly septate, and 11-22 by 2.3-3.4 microns (Fig. 8).

On old scald lesions collected in July and August, sporodochia were frequently found (Fig. 7). They had developed through the stomates over large areas of the lesion. Spores from such fruiting structures were identical with those produced singly on the young lesions.

Cultures of the fungus produced a very sparse mycelium which was soon obscured by a pink mass of conidia. The conidia were produced over the entire surface of the colony.

Selenophoma bromigena (Sacc.) Sprague and Johnson

Sprague, R. and A. G. Johnson. Species of Selenophoma on North American grasses. Oregon State Coll. Monographs Bot. 10. 1950.

Spots are circular to irregular, gray with narrow brown borders, and may enlarge and coalesce to form irregular blotches of necrotic tissue (Fig. 9). Pycnidia form readily throughout the lesion. The symptoms may vary somewhat in the latter part of the season on foliage developing after the first cutting. In some cases the tip of the leaf was killed completely, and later scattered pycnidia developed in the necrotic tissue. The mature pycnidia frequently drop out of the host tissue, leaving holes in the lesions. Selenophoma leaf spot is most prevalent in the spring, not spreading to any extent during the later summer months. It may become prevalent on new fall growth.

The pycnidia are spherical to subglobose, light golden brown, ostiolate, 50-150 microns in diameter (Fig. 10). The conidiophores are prominent, truncate to flask shaped, 3-5 by 2.5-3.5 microns. Spores are regularly lunate, hyaline, nonseptate, 17-25 x 2-2.3 microns (Fig. 11).

S. bromigena grows slowly in culture, producing pycnidia and conidia in a mounded, irregular colony. The spores germinate quickly and the colony becomes overgrown with mycelium.

Stagnospora bromi Smith and Ramsb.

Sprague, R. Some leafspot fungi on western Gramineae IV. Mycologia 41:493-504. 1949.

Typical Stagnospora leaf spots are elongate, purple brown, with the center of the lesion becoming paler as it ages (Fig. 12). Lesions that closely resemble those of Helminthosporium bromi have been observed frequently during the summer. They were dark brown with a marked halo, but when such lesions were examined in the laboratory or with a hand lens in the field, pycnidia of Stagnospora bromi were observed. The pycnidia commonly seemed to be deeper in the mesophyll of the leaf than were those of Selenophoma bromigena, and were thus more difficult to distinguish macroscopically. The number of pycnidia developed in a single lesion was usually small.

The pycnidia are brown, globose-lenticular and 130 to 175 microns in diameter (Fig. 13). Spores are fusiform to subcylindric, straight to curved, three septate, nonconstricted at the septa, and 17-24 by 2.7-3.6 microns (Fig. 14). Young spores are nonseptate, while slightly older ones possess a single central septum. Often the final two septa are formed late in the maturation of the spores, a fact which sometimes is confusing when one is attempting to differentiate among the various pycnidial fungi which occur as parasites and saprophytes on brome.

In culture, Stagnospora bromi grew well on a wide range of media, producing a white to gray low-growing mat of mycelium. Pycnidia and conidia were produced sparsely on any of the artificial media used, but were produced in abundance in two weeks on sterile brome stems or leaves. Conidia in water germinated one hundred per cent throughout the temperature range from 7°C to 30°C. The initial germ tubes were usually formed from the terminal cells of the spores, but germ tubes were sometimes produced later from the central cells also.

Septoria bromi Sacc.

Sprague, R. Septoria diseases of Gramineae in western United States. Oregon State Coll. Monographs. Bot. 6. 1944.

Spots are brown, elliptical to elongate, sometimes appearing to be limited in lateral spread by the larger veins (Fig. 15). Yellow areas surrounding the spots are common. Pycnidia are formed throughout the lesion, and are not as prominent as are the pycnidia of Selenophoma. In both fungi the pycnidia form under a stomate, they tend, therefore, to be oriented in rows in the lesion.

Pycnidia are brown to black, spherical to flattened, 60-120 microns (Fig. 16). Conidiophores are narrowly ampulliform to subcylindric, and 5-7 by 1.5-2 microns.

Spores are characteristically whip-like, narrowly filiform-clavulate, usually two septate, 33-65 by 1.2-2.5 microns (Fig. 17).

Septoria jaculella Sprague has also been reported on Bromus inermis, but it differs in its longer, javelin-like spores. No collections of S. jaculella have been made in Iowa.

In culture, S. bromi grew slowly on all media used. If conidial suspensions were used as inoculum and plates heavily seeded, quantities of pycnidia and conidia were produced in ten days. Conidia in water germinated one hundred per cent throughout the temperature range from 15°C to 28°C. Germ tubes formed from the ends of the spores; also occasionally several formed from the central portion. Some germination occurred at 10°C and above 30°C, but those that did germinate outside of this temperature range formed swollen, distorted germ tubes.

Hendersonia crastophila Sacc.

Sprague, R. Diseases of cereals and grasses in North America. Ronald Press Co., New York. 1950.

This fungus has been reported on Bromus inermis, B. tectorum L. and various other grasses as a saprophyte and weak parasite on crown and culm, and also as a factor in a leaf rot without definite spotting. It has been collected here frequently on culms and old leaves of B. inermis in the fall.

Pycnidia are sunken, with the basal portion more or less globose, brown, firm walled, 90-360 microns in diameter (Fig. 18). The neck varies in length, and at maturity the ostiolar region has a few scattered stiff spines. The development of the spines varies greatly.

Spores are yellow-brown, curved, spindleform to nearly straight, slightly flattened on one side, seven septate, 24-45 by 3-5 microns (Fig. 19).

Inoculation experiments in the greenhouse were successful only on older, senescent leaves.

Ascochyta sorghi Sacc.

Sprague, R. and A.G. Johnson. Ascochyta leaf spots of cereals and grasses in the United States. Mycologia 42:523-553. 1950.

Lesions are circular to elliptical, brown or fawn colored, usually with red or thin brown discolored borders. They occur mainly on lower leaves or on the leaf tips. The only collections of Ascochyta lesions in Iowa have been made in the early spring. However, abundant pycnidia of A. sorghi have been found throughout the season on dead leaves and culms.

The pycnidia are subglobose, erumpent, golden brown with darker oxidized cells adjacent to the ostiole, and 90-140 microns in diameter (Fig. 21). Spores are subcylindric to ovate, fusoid, variable in size, 11-21 by 1.6-4 microns (Fig. 20). In water, spores germinated one hundred per cent throughout the temperature range from 10°C to 30°C. Germ tubes were formed from both cells of the spores. No germination occurred at 4°C or at 35°C. A. sorghi grows well in culture on various media, producing a dirty white mycelial growth; pycnidia, however, were produced only on sterilized plant tissues.

Colletotrichum destructivum O'Gara

Tiffany, L.H. Colletotrichum destructivum on brome grass (Abst.) Phytopath. 43:486. 1953.

Isolates of C. destructivum were obtained from basal necrotic lesions on leaves of brome collected in an alfalfa-brome grass pasture near Ames. Setose acervuli are produced abundantly in the lesions (Fig. 22).

The conidia are straight, hyaline, unicellular, rounded at apex and bluntly pointed at base, 14-18 by 3.5-4.5 microns (Fig. 23).

In culture, organized acervuli are not formed on regular culture media. An olive-green to black subsurface mycelium is produced, from which originate scattered black setae and conidiophores over the surface of the entire colony. The isolates were pathogenic on brome grass in greenhouse inoculations.

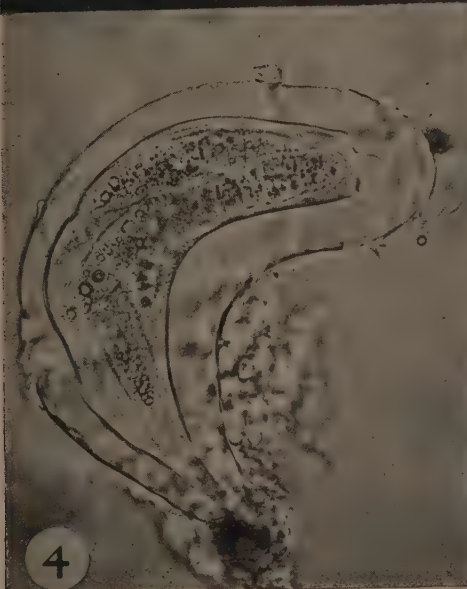
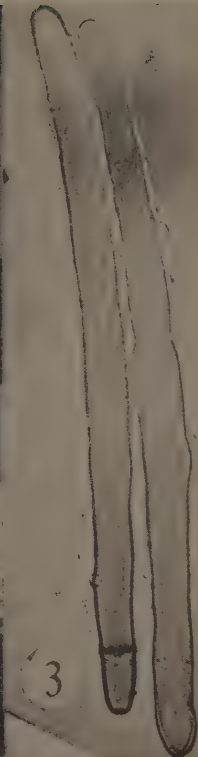
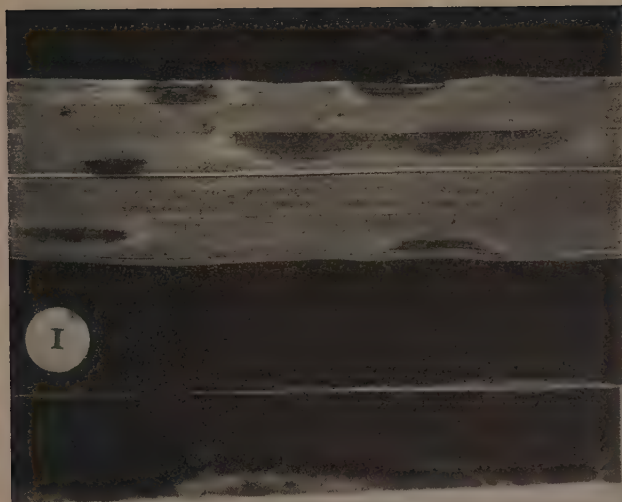
SUMMARY

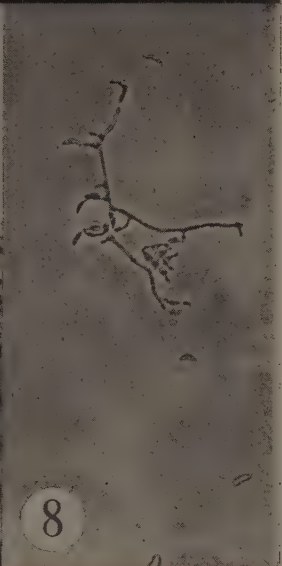
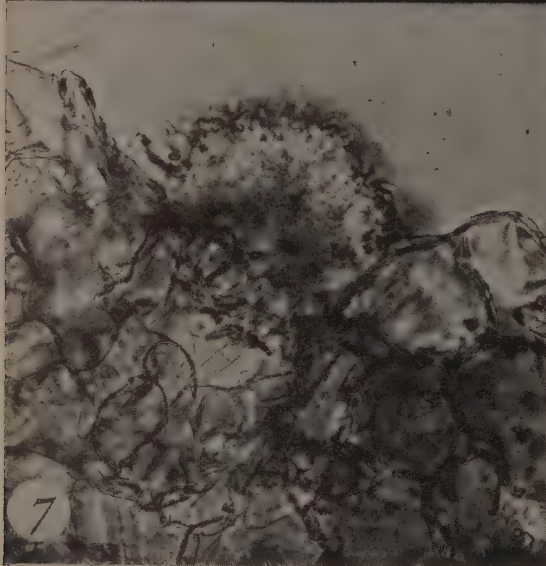
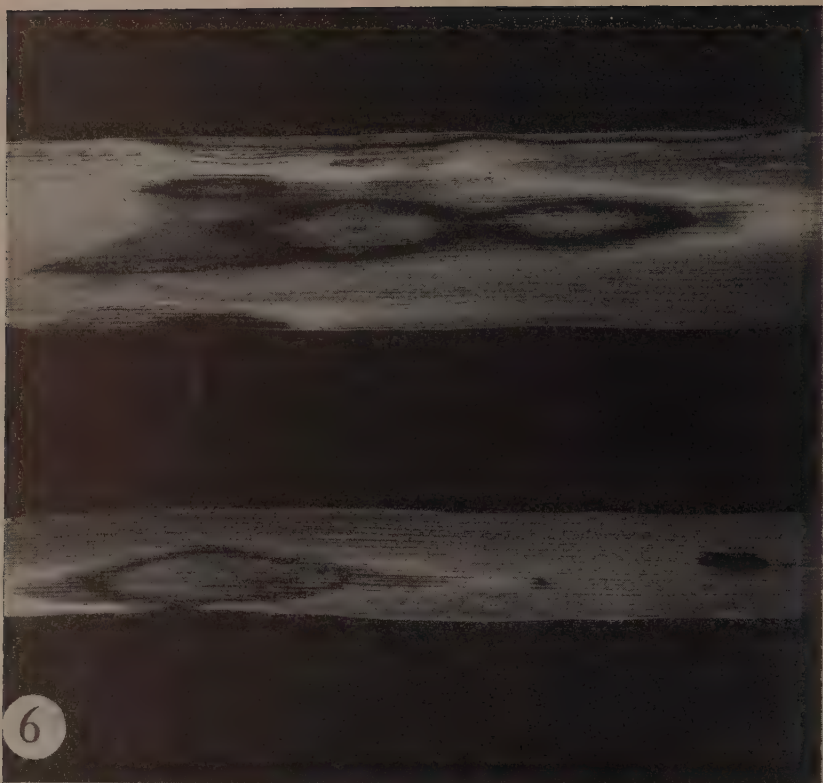
Of the common prevalent leaf spots, those caused by Selenophoma and Septoria can be readily differentiated from any of the others by virtue of the numerous dark pycnidia in the lesions. The Septoria leaf spots tend to be limited in width by the veins, resulting in a rectangular, blocky lesion. The Selenophoma spots are commonly circular, oval to irregular, and gray in color. Rhynchosporium leaf spots, which are commonly called scald, are also gray, but different in general aspect. They are initially somewhat oval, but enlarge and elongate to include extensive areas of the leaf.

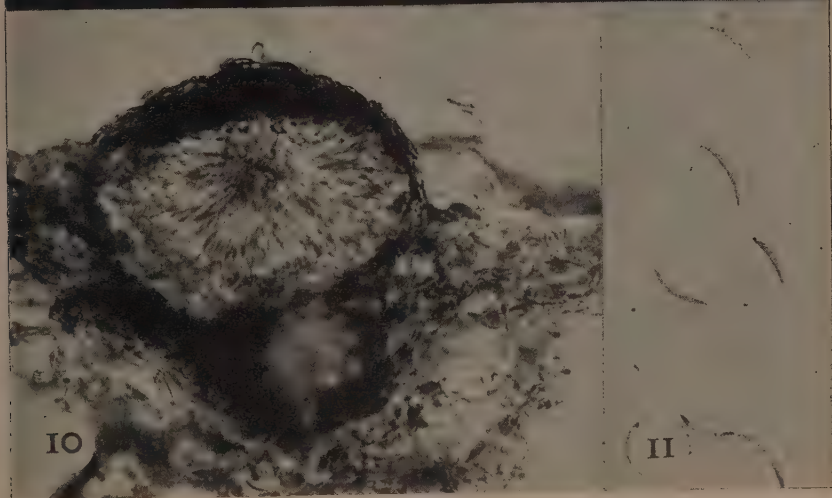
The Helminthosporium lesions, commonly designated as brown leaf spot, are dark brown to black with a yellowish halo. The halo may be lacking in very young lesions. They are somewhat limited in width by the larger leaf veins, but may elongate and coalesce to cover larger areas of leaf surface. There are two other leaf spots which may be confused with Helminthosporium leaf spot in certain stages of development. Early stages of lesions caused by Xanthomonas translucens (Jones, Johnson, and Reddy) Dows. may be confused, but on older lesions the crust of bacterial exudate is an effective diagnostic characteristic. During the summer Stagnospora lesions frequently resemble either of the two previously mentioned spots, but can usually be differentiated by the brown Stagnospora pycnidia in the lesions.

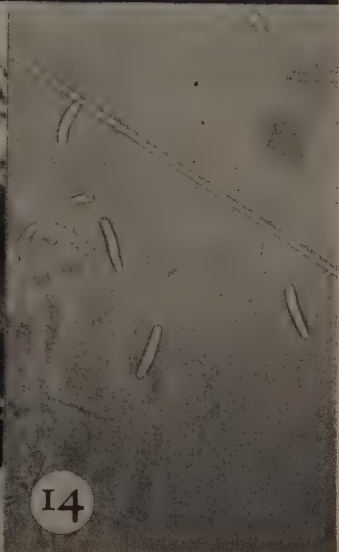
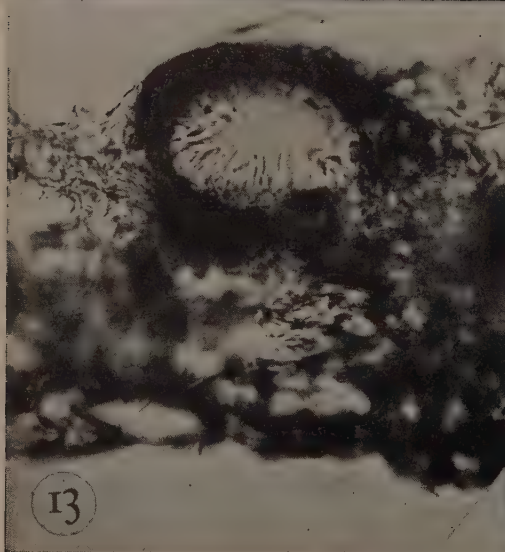
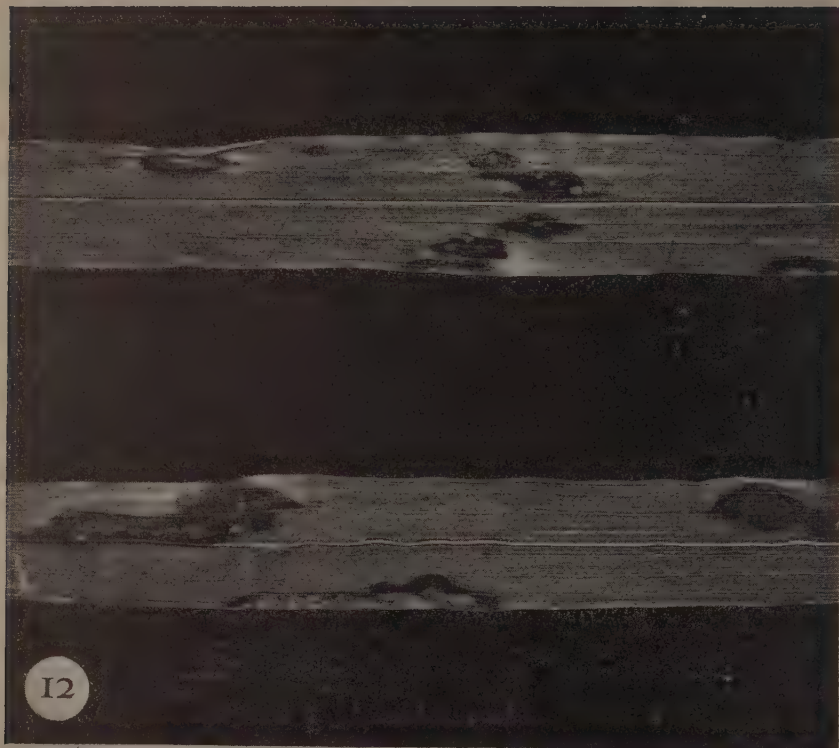
Hendersonia and Ascochyta are not so commonly encountered as parasites on actively growing leaves, and would be a source of confusion only in the consideration of lesions on mature to senescent leaves. The spots caused by Hendersonia are vague and indefinite, and hence not difficult to distinguish from the others. The Ascochyta lesions are distinctive in aspect as discussed previously. They have been found rarely, and then only on lower leaves or on leaf tips.

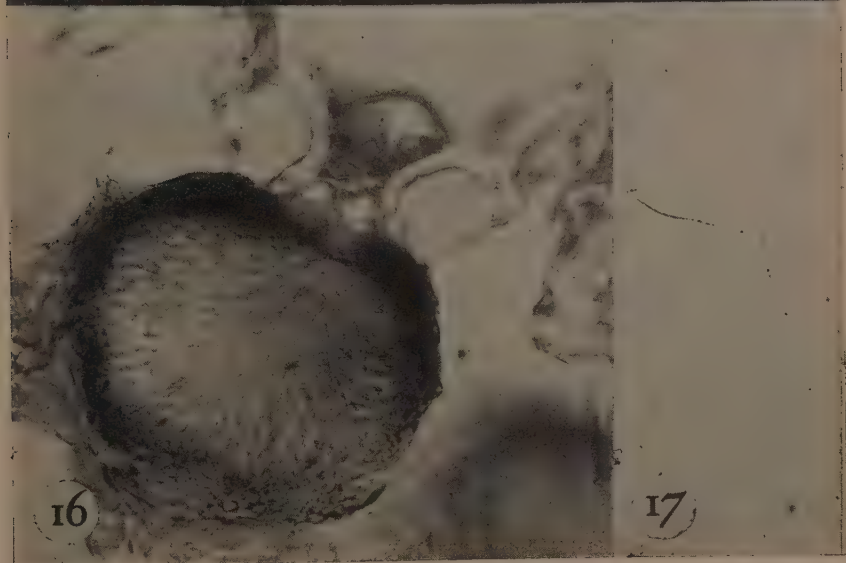
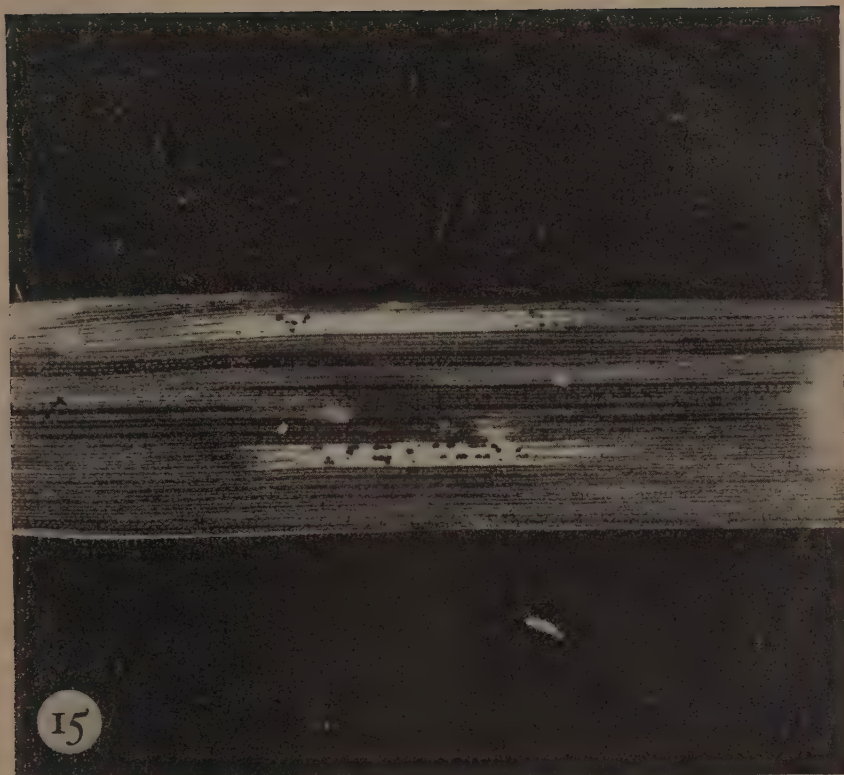
- Figs. 1-5. Pyrenophora bromi. 1. Lesions on brome leaf.
2. Perithecia (X12). 3. Conidia (X450).
4. Young ascus (X450). 5. Mature ascus (X450).
- Figs. 6-8. Rhynchosporium secalis. 6. Lesions on brome leaves.
7. Sporodochium on old lesion (X450).
8. Conidiophores and conidia (X450).
- Figs. 9-11. Selenophoma bromigena. 9. Lesions on brome leaves.
10. Cross section of a pycnidium (X450).
11. Conidia (X450).
- Figs. 12-14. Stagnospora bromi. 12. Lesions on brome leaves.
13. Cross section of pycnidium (X450).
14. Conidia (X450).
- Figs. 15-17. Septoria bromi. 15. Lesions on brome leaf.
16. Cross section of pycnidium (X450).
17. Conidia (X450).
- Figs. 18-19. Hendersonia crastophila. 18. Pycnidium (X450).
19. Conidia (X450).
- Figs. 20-21. Ascochyta sorghi. 20. Conidia (X450).
21. Pycnidium (X450).
- Figs. 22-23. Colletotrichum destructivum. 22. Acervulus (X450).
23. Conidia (X450).



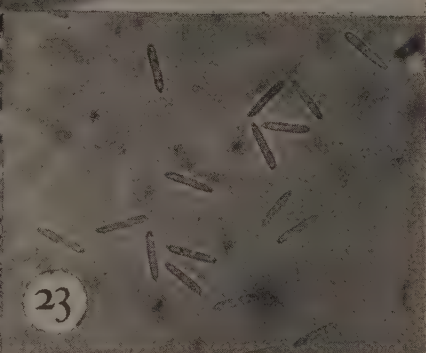
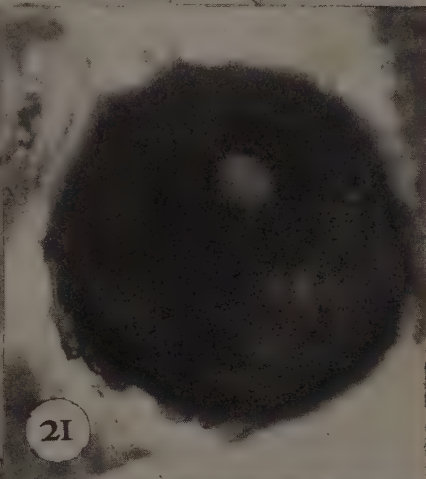
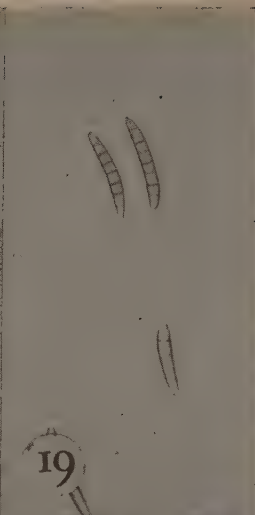








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THE LEGUMINOSAE OF THE NORTH-CENTRAL UNITED STATES
II. HEDYSAREAE¹

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The scope and purpose of investigations on the legumes of the north-central³ states are detailed in a previous paper (Isely, 1951a). An attempt is made to treat all leguminous species within this region, native, cultivated, and/or naturalized. These reports are intended not only to provide a means of quickly identifying the plants concerned, but also to serve as a source of information (insofar as such information is available) in regard to the distribution, relationships, habitat characteristics, biology, and agricultural employment of the species.

No attempt is made to give complete synonymy for the species treated. Synonyms are listed only for those plants which have been designated by more than one name in current or well-known manuals or state floras. These synonyms are cross-indexed at the end of the treatment. Common names are listed for those species having well established names which are actually used. The author is not in sympathy with the prevalent tendency to coin artificial so-called common names for all plants.

Acknowledgements

In the course of the present study, the author employed the herbarium facilities, or borrowed specimens, from the following institutions: Iowa State College, Chicago Museum of Natural History, Missouri Botanical Gardens, and the University of South Dakota. The kindness of the respective curators is acknowledged with thanks.

The author especially appreciates the cooperation rendered by Mrs. Elsie Froeschner in preparing the illustrations, and by Mr. and Mrs. David McClure in assisting with technical details.

HEDYSAREAE

Plants mostly perennial herbs. Leaves stipulate, predominately trifoliate; some genera with pinnately compound blades. Leaflets entire, with or without stipels. Inflorescence paniculate, of axillary flower

¹Journal paper No. J-2355 of the Iowa Agricultural Experiment Station, Project 1073.

²Illustrations by Mrs. Elsie Froeschner

³The north-central United States are defined to include North Dakota, South Dakota, Nebraska, Kansas, Missouri, Iowa, Minnesota, Wisconsin, Illinois, Indiana, and Michigan.

clusters, or umbellate (Coronilla). Calyx tubular, deeply or shallowly 3-5 toothed or lobed (teeth 5 but often variously fused and appearing fewer in number), frequently somewhat 2-lipped. Corolla papilionaceous, usually pink to purple, sometimes yellow (Arachis, Stylosanthes) or white. Stamens diadelphous or (less commonly) monadelphous. Pod an indehiscent loment, constricted into one or several one-seeded joints which usually separate at maturity.¹

The Hedysareae, one of the major groups of the Leguminosae, contain 40-50 genera and possibly 1000 species. Its members are to be found on all continents. Of these, six genera containing approximately 70 species are native to North America north of Mexico; representatives of 5 additional genera have been introduced. The present study treats 7 genera and 38 species occurring in the north-central states.

The Hedysareae are defined on the basis of pod characteristics; it is difficult to delimit the group on any additional or supplementary basis. The flowers, for instance, usually possessing a papilionaceous corolla and diadelphous stamens, are essentially similar to those of the majority of the more advanced Papilionoideae. However, the stamens in certain genera are monadelphous, (Desmodium possesses both monadelphous and diadelphous representatives), and Adesmia has free stamens. The leaves are pinnately trifoliate in the major North American genera, Desmodium and Lespedeza, but may be odd-pinnate with numerous leaflets (e.g., Hedysarum, Coronilla), or even-pinnate with four leaflets (Zornia, Arachis). Inflorescence structure within the tribe is apparently diverse. For instance, in Desmodium and Lespedeza, the fundamental units appear to be reduced cymules or dichasial clusters which are variously aggregated into panicles, head-like or axillary clusters. On the other hand, Coronilla, with an umbellate inflorescence similar to that of Lotus, shows little evidence of a dichasial association of the individual flowers. The loment segments are variable; they are compressed in genera such as Desmodium and Lespedeza, but are quadrangular in Aeschynomene and Coronilla; the loment segments separate at maturity in Desmodium but fail to do so in Arachis and Stylosanthes; the pod is reduced to a single one-seeded segment in Lespedeza. To a large extent, the subtribes (Desmodiinae, Stylosanthinae, Aeschynomeninae, Patagoniinae, Coronillinae and Euhedysarinae) are characterized on the basis of these variable characteristics.

The Hedysareae, being arbitrarily defined on the basis of the indehiscent, jointed nature of the pods, are almost certainly not a natural group in the evolutionary sense. The development of indehiscent, jointed fruits has not been limited to a single group in the course of the history of the Leguminosae - the incipient tendency is observable in several tribes. The Hedysareae then probably represent an aggregation of extremes or

¹The above is a characterization of the Hedysareae found in North America. Some qualifications would be required, were the tribe to be defined on a world-wide basis. The most recent summary of the tribe as a whole is that of Taubert (1894).

evolutionary end-points in loment structure, and doubtless include representatives from several developmental lines within the Leguminosae. The above viewpoint is not original with the present author; it has been espoused by several others. For instance, Gams (1923-24) believes the tribe to be polyphyletic, hypothesizing derivation of various subtribes as follows: the Desmodiinae (Desmodium, Lespedeza), and Hedysarinae (Hedysarum) from primitive Galegeae; the Coronillinae (Coronilla) from the Loteae; the Stylosanthinae (Stylosanthes) from the Dalbergieae, and Adesmia from the Sophoreae. Senn (1938) states that certain of Gams' conclusions based on morphological data are supported by serological and cytological investigations. Dormer (1946) correlated the presence or absence of foliar pulvini with the vascular anatomy and distribution of various leguminous groups, concluding that the Hedysareae is "undoubtedly an unnatural group, and the subtribes need to be redistributed among the other groups of the Papilionatae." Dormer suggests specifically that the Loteae (Lotus, Dorycnium, Securigera, Anthyllis) and Coronillinae (Coronilla, Hippocrepis, Ornithopus) constitute a single group which "should be combined." It is suggested that the Desmodiinae are derived from the Psoralinae; certain similarities between Amorpha and Lespedeza are emphasized.

Kunth (1908) describes the pollination mechanism of Coronilla varia, a specialized pumping arrangement which is essentially the same as that of Lotus.

Key to the Genera of the Hedysareae¹

1. Leaves with more than three leaflets
 2. Leaflets four; flowers yellow; fruit matured underground. (Plate I, Fig. 1) Arachis
 2. Leaflets nine or more; flowers white to purple; fruit matured above ground. (Plate X, Figs. 2, 5)
 3. Flowers in umbellate clusters; loment 4-angled; stipules inconspicuous. (Plate I, Figs. 2, 3). Coronilla
 3. Flowers in axillary racemes; loment flattened or one-seeded; stipules conspicuous, marginally connate. (Plate X, Figs. 1-6; Plate XIX, Figs. 1, 2)
 4. Pods several-jointed and seeded; wings about as long as other petals; leaflets with inconspicuous or conspicuous lateral nerves; plants native. (Plate X, Figs. 1-6). Hedysarum

¹ This key is based on characteristics of members of the various genera found in the north-central United States. Somewhat broader generalization would be required were the genera as a whole under consideration.

4. Pods with a single joint and seed; wings considerably shorter than other petals; leaflets with conspicuous lateral nerves; basal leaves usually aggregated in a rosette; plants introduced and sporadic in occurrence. (Plate XIX, Figs. 1,2) Onobrychis

1. Leaves with three leaflets.

5. Loments flattened; flowers purplish to white; stipules not fused to leaf base. (Plate II, Figs. 1-2 et al.)

6. Plants in fruiting condition.

7. Loments of a single, one-seeded segment. (Plate XI, Fig. 4 et al.) Lespedeza

7. Loments with 2-several segments and seeds. (Plate II, Fig. 1 et al.) . . . Desmodium

6. Plants in flowering or vegetative condition.

8. Stipels evident on leaves, stem pubescence frequently containing or consisting of hooked hairs; calyx not bracteate. (Plate II, Fig. 8) Desmodium

8. Stipels absent; stem pubescence usually of straight or curved hairs. (Plate III, Fig. 3; Plate XI, Fig. 2)

9. Calyx with 2 or 3 closely subtending bracts; principal leaflets less than 3 cm. in width; leaves not clustered; plants various in habitat, rarely of dense or rich woodlands. (Plate XI, Figs. 2-5 et al.) Lespedeza

9. Calyx not bracteate; principal leaflets more than 3 cm. in width; woodland species usually with clustered leaves. (Plate III, Figs. 1-3) Desmodium
(D. glutinosum, nudiflorum, pauciflorum)

5. Loments not flattened; flowers yellow or orange; stipules fused to leaf base. (Plate XIX, Figs. 3-5) Stylosanthes

ARACHIS L.

Leaves even-pinnate with four leaflets. Flowers yellow, axillary, borne at the apex of a stipe-like calyx tube. Stamens monadelphous. Basal portion of pistil elongating and geotropic after anthesis; ovary maturing beneath the soil. Legume indehiscent, thick and fib-

rous, terete, somewhat constricted between the two (sometimes one or three) seeds. Seeds ovoid with a thin, membranous seed coat.

Arachis, a genus of about ten species, is native to South America.

Literature

Hermann (1954). A synopsis of the genus Arachis.

Smith (1950). Structure of flower and fruit.

ARACHIS HYPOGAEA L. Peanut (Plate I, Fig. 1. Map 1)

Plants ascending or decumbent. Stipules conspicuous, pointed, fused to petiole base. Leaflets obovate.

The peanut presumably was originally native to Brazil. It now occurs in cultivation in Asia, Africa, Mediterranean Europe, and the south-central and eastern United States. It is grown to a limited extent in southern Kansas and Missouri and may occasionally be found as an escape.

Smith (1950) has described the gross morphology of the flower and fruit of the peanut in detail, and corrected several misconceptions in past literature.¹ He points out that the floral parts are borne at the apex of a stipe-like calyx-tube (hypanthium), but that the flower is morphologically sessile. The stamens are monadelphous, eight fertile and two sterile. The flowers are usually self-pollinated. The geotropic stipe or "peg" which appears after anthesis is an elongation of the base of the ovary; the fertilized ovules are borne in the tip of this peg which grows vertically downwards and penetrates the soil for 2-6 cm.

Previous authors have described two types of flowers borne by the peanut, aerial (as above described), and cleistogamous underground flowers. Various statements have been made as to the relative fertility of these two types. Smith (l.c.) states that the flowers are all of the same type and that subterranean flowers "do not represent an inherent evolutionary trend toward cleistogamy but merely a response to the environment created by the farmer's plow.", i.e., lower nodes are frequently buried by cultivation, and flowers subsequently developed fail to open naturally.

Numerous determinations (Senn, 1938) have indicated a gametic chromosome number of 20 for the peanut; two authors (cited by Senn) have reported 10.

The peanut was employed as a food plant by various South American Indians before the coming of the white man. It was transported to Europe and North America in the early colonial days, but remained a relatively minor crop until the beginning of the present century. During the last twenty years, it has become increasingly important in the agriculture of the southern states, due to the increased diversity of uses for peanut products, and to the trend away from a one-crop (cotton) agriculture.

The direct employment of "roasted" peanuts as human food is well known. Peanuts are used in commerce in making peanut butter and in

¹This author cites a large volume of literature on the peanut which will not be duplicated here.

the manufacture of vegetable food oils. The plant, exclusive of the nut, is valuable for forage and hay. In the southeastern states it is one of the more important hog foods; in many cases, the animals are merely turned loose in the fields where they harvest both the tops and the nuts. In parts of Alabama and Georgia, corn and peanuts are planted together; after harvest of the corn the peanuts are hogged-off or harvested.

CORONILLA L.

Herbs or low shrubs. Leaves pinnately compound (one species unifoliolate). Flowers umbellate, yellow, less frequently reddish. Calyx nearly regular. Stamens diadelphous. Loment terete or quadrangular, constricted between seeds.

This genus is composed of about 20 species, native, for the most part, to Mediterranean Europe and adjacent Africa. Although ordinarily included in the *Hedysareae* on the basis of its loment-like pods, its relationships are probably with the *Loteae*. (Page 34)

Literature

Gams (1923-24, 1465-1475). European species.

CORONILLA VARIA L. Crown vetch (Plate I, Figs. 2,3. Map 2)
Plant perennial, erect or ascending. Stems glabrate, branched. Leaves pinnately compound with 11-21, subsessile, oblong leaflets. Stipules inconspicuous. Umbels on long, axillary stalks, usually 10-15 flowered. Corolla pinkish, drying lavender, rarely white. Loments woody, somewhat curved, beaked, jointed or constricted between the 3-7 segments.

Coronilla varia is native to middle and southern Europe - Spain to the Balkans, north to central Germany -, and adjacent Asia - Syria, Persia, Asia Minor. In the United States it is sporadically naturalized in open areas and along roadsides in the north-central and north-eastern states (also reported from western Oregon), and is occasionally employed as an ornamental. Flowering takes place in late June or early July. Deam (1940) comments upon the weedy potentialities of this plant due to its ability to spread from underground stems.

Crown vetch is variable as regards pubescence, leaflet size and shape and flower color; these characters have been accorded various varietal and form names in European literature (e.g., Gams 1923-24).

DESMODIUM Desv. Tick-Trefoil (Meibomia Adans.)

Woody or herbaceous perennials, or annuals - ours all herbaceous perennials. Stems usually with hooked hairs. Stipules subulate to deltoid, deciduous or persistent. Leaves (in our species) pinnately trifoliolate,



PLATE I, ARACHIS AND CORONILLA

Arachis hypogaea, 1. Leaf and stipule $\times 2/3$.

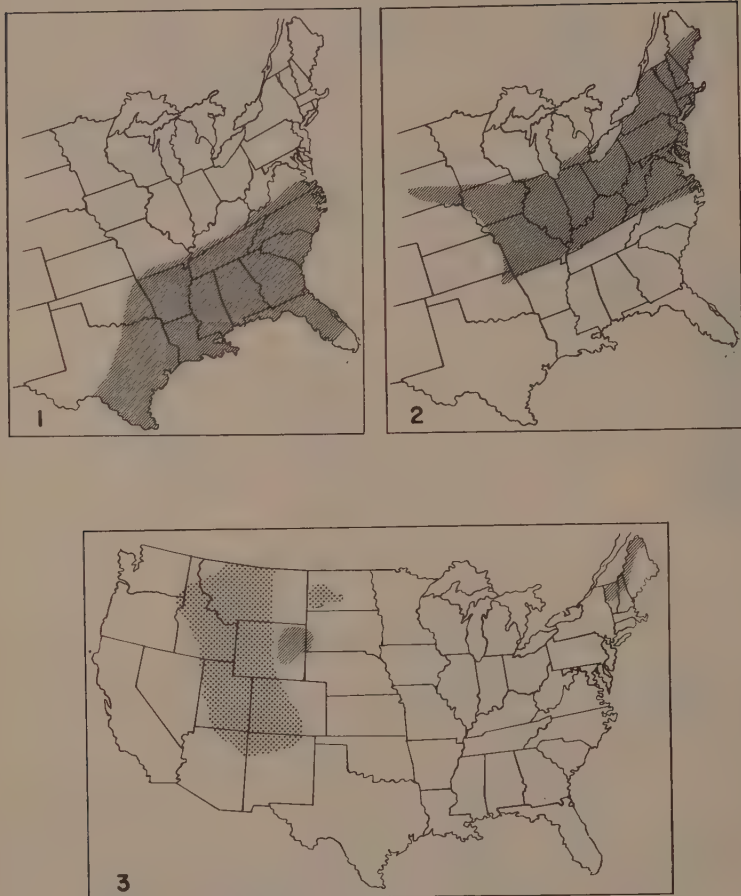
Coronilla varia, 2. Mature fruit $\times 2$. 3. Flower cluster $\times 1-1/3$.

usually stipellate. Inflorescence racemose or paniculate; axis pubescence including, or consisting entirely of, hooked hairs. Calyx lobed or shallowly toothed, usually somewhat two-lipped. Wings somewhat coherent. Stamens diadelphous or less frequently monadelphous. Pod indehiscent, the basal portion narrowed into a stalk¹ approximating or exceeding the calyx; seed-bearing portion flattened and constricted into 2-8 one-seeded joints or segments; incisions between joints usually deeper on ventral margin than dorsal, the isthmi thus more or less dorsal; segments glutinous-pubescent with hooked hairs, separating at maturity.

Desmodium, a polymorphous genus of between 150 and 200 species is to be found on all major land masses; it is lacking only in the western half of the United States, continental Europe, and New Zealand.

The unity of most large genera has been subjected to question at one

¹In descriptions of species the 'stalk' refers to this portion of the pod, not to the pedicel.



1. *Arachis hypogaea*. 2. *Coronilla varia*. Also reported on ballast, Portland, Oregon. 3. *Hedysarum*, *H. alpinum*, hatched; *H. boreale*, stippled.

time or another; *Desmodium* is no exception. The German worker Schindler (1924, 1924a, 1926, 1926a) has segregated several genera from *Desmodium* proper including (1924) a major operation, dividing the genus into two large groups, *Desmodium* and *Meibomia*.¹

¹To avoid confusion, it should be noted that this usage of *Meibomia* differs from that of proponents of the American code of nomenclature (e.g. Britton and Brown, 1913; Small, 1933; Rydberg, 1932) who have employed it in place of *Desmodium*.

Following this interpretation, all of the eastern American species would belong to the genus Meibomia except for Desmodium glutinosum, nudiflorum and pauciflorum. There is considerable weight of evidence favoring adherence to this viewpoint. However, subsequent authors have not followed Schindler, but have adhered to the more traditional classification - possibly, in part, because a proper evaluation of Schindler's conclusions would call for a world-wide knowledge of the genus.

Regarding the relationships of the American Desmodia, two groups, in a phylogenetic sense, may be distinguished. Except for three species, the central and eastern United States representatives of the genus are allied with southwestern and Mexican species; the center of distribution of this complex may be tropical America. The other group, consisting of the plants enumerated in the above paragraph, is of Asiatic affinities. These species differ from their American congeners not only in their obvious relationships, but in a number of morphological characteristics, e.g., the nature of the calyx, the stamens (monadelphous vs. diadelphous), obsolescence of stipels, and the character of the loment and seeds. This section of the genus has been treated in detail by Isely (1951).

In the United States, the common names tick-trefoil, stick-tights, beggar-lice, beggar-weeds, and beggar-ticks are variously applied to members of the genus Desmodium. Tick-trefoil is perhaps the most widely used. All of these names take their origin from the tendency of the mature loment segments to adhere to clothing or to the hair of animals.

All of the American species of Desmodium are herbaceous perennials. Most of them possess thick, woody crowns and a ligneous, perennial root system. Most of them grow in light, sandy, or sterile soil, and are usually found in open woodlands or at the edge of more densely shaded areas. Like many other native legumes, they may act as pioneers in the revegetation of denuded, burned over, or eroded areas, gradually disappearing as the vegetational cover, particularly that of shading plants, increases. Graham (1941) cites numerous records indicating that the native Desmodia are "of prime importance to wild life." One species, the so-called Florida beggar-weed (Desmodium tortuosum (Sw.) DC.) is grown to a limited extent in the southeastern states for green manure and forage, and a number of others are similarly employed in the tropics. For instance, Hosaka and Ripperton (1944) discuss five species of Desmodium which appear to be of major importance on Hawaiian ranges.

Fassett (1939) emphasizes pubescence characters in identifying members of this genus, and an accompanying study by Mose (1939) describes and illustrates the various kinds of trichomes found on the Wisconsin members of the genus.

Senn (1938) indicates a basic chromosome number of 11 for all species studied. Young (1940) has tabulated chromosome determinations for over twenty species (primarily American) of Desmodium, and briefly described chromosome morphology. He found a gametic number of 11, or somatic 22 for all species studied.

Literature

- Dearn (1940, 603-610). Indiana spp.
Fassett (1939, 80-98). Wisconsin spp.

- Fox (1945, 222-224). Iowa spp.
 Graham (1941, 48-51). Use by wild life.
 Isely (1951). Section Podocarpium.
 Isely (1954). D. paniculatum and viridiflorum.
 Jones (1945, 165-167). Illinois spp.
 Schubert (1950). Taxonomic notes, eastern U.S.
 Schubert (1950a, 915-923). Eastern U.S.
 Schindler (1924, 1924a, 1926, 1926a). Generic limits; descriptions and notes concerning species on a world-wide basis.
 Rydberg (1932, 487-490). Central United States, as Meibomia.
 Young (1940). Cytology.

Key to Species of Desmodium

1. Calyx lobes much shorter than tube; loment long-stalked above calyx; ventral margin of loment incised almost to dorsal suture. (Plate VI, Figs. 1-3)
 2. Loment stalk 9-10 mm. long; pedicels 1-2 cm. in length; inflorescence scapose, rarely leaf-bearing. (Plate VI, Figs. 1-3) . . . Desmodium nudiflorum
 2. Loment stalk 4-6 mm. long; pedicels stout, less than 1 cm. in length; inflorescence borne on the leafy stem. (Plate III, Figs. 1-3)
 3. Stems erect, unbranched below inflorescence; leaves usually clustered; terminal leaflets as broad or broader than long, conspicuously acuminate; inflorescence strongly exserted above leaves; flowers usually pink. (Plate III, Figs. 1-3). D. glutinosum
 3. Stems ascending or sprawling, branched; leaves dispersed over stem; terminal leaflet usually longer than broad, weakly acuminate; inflorescence scarcely exserted above leaves; flowers white. (Plate VII, Figs. 1-2). D. pauciflorum
1. Calyx lobes equalling or longer than tube; loment sessile or slightly stalked above calyx; ventral margin of loment various, usually incised one-half to three-fourths loment width. (Plate II, Fig. 1)
 4. Plants prostrate vines. (Plate V, Fig. 6; Plate IX, Fig. 1)
 5. Terminal leaflets suborbicular; flowers pinkish. (Plate IX, Fig. 1). . . . D. rotundifolium
 5. Terminal leaflets ovate; flowers yellowish-white. (Plate V, Figs. 6-7). . . D. ochroleucum
 4. Plants not prostrate vines.

6. Pubescence on leaf blades of hooked trichomes; stipules ovate-deltoid, 3-5 mm. broad at base and semi-clasping. (Plate IV, Figs. 1, 4)
7. Loment segments 4-6 (7) mm. long, rounded on both sutures; inflorescence simple or slightly branched, glutinous-pubescent with short, glandular hairs; stipules not reflexed. (Plate IV, Figs. 1-4). . . D. illinoense
7. Loment segments 6-12 mm. long, angled on ventral suture; inflorescence branched or compound (or simple on depauperate plants), villous-hirsute; stipules frequently reflexed. (Plate II, Figs. 6-8). . . D. canescens
6. Hairs on leaf blades not hooked (except sometimes for a few along nerves); stipules subulate to lanceolate, 0.5-3.0 mm. wide, not clasping, frequently deciduous, (Plate II, Figs. 2-3)
8. Loments predominantly 2 (3)-segmented, the joints rounded ventrally; flowers small, 3-6 mm. in length. (Plate II, Fig. 4)
9. Leaflets narrowly oblong to linear; leaves subsessile; pedicels not exceeding 5 mm. (Plate IX, Figs 2,3) D. sessilifolium
9. Leaflets broadly ovate to oblong-lanceolate; blades petiolate to subsessile; pedicels usually exceeding 5 mm. (Plate II, Fig. 5; Plate VIII, Fig. 6)
10. Leaflets ovate to elliptic, of essentially the same size, usually not exceeding 3 cm. in length; stipules subulate, deciduous or persistent; bracts subulate. (Plate II, Fig. 5)
11. Pedicels (8) 10-15 mm. long, slender, frequently somewhat arcuate; plants glabrate or sparsely hirsute; petioles mostly 1.5-2.5 cm. (uppermost may be shorter); leaflets usually ovate. (Plate V, Figs. 1,2) D. marilandicum
11. Pedicels 5-9 mm. long, stiff; plants hirsute; petioles mostly 0.5-1.0 cm. long (lowermost may be longer); leaflets usually elliptic. (Plate II, Figs. 4,5) D. ciliare
10. Leaflets ovate to lanceolate, the terminal one frequently 4-6 cm. long

- and conspicuously longer than lateral; stipules lanceolate, conspicuous but early deciduous; bracts conspicuous before anthesis. (Plate VIII, Fig. 6) D. rigidum
8. Loments predominantly (3) 4-6 segmented, the ventral suture with rounded or angled incisions; flowers various, usually exceeding 6 mm. in length. (Plate II, Fig. 1)
12. Loment segments angled beneath except D. nuttallii with velvety-tomentose leaves), 4-7 (8) mm. long; stipules and bracts frequently subulate; flowers in most species 5-6 mm. long. (Plate IX, Fig. 4)
13. Leaves velvety-tomentose beneath; bracts pilose, usually deltoid and broad at base; stipules frequently brick-red in color. (Plate IX, Fig. 5)
14. Loment 4-5 jointed, nearly straight, the segments 5-7 (8) mm. in length, usually angled below; leaflets broadly ovate, the terminal one frequently exceeding 10 cm. in length. (Plate IX, Figs. 4,5) D. viridiflorum
14. Loment 3-4 jointed, usually curving inwards; segments 3.5-5.0 mm. in length; roundish; leaflets ovate to elliptic, rarely reaching 10 cm. in length, (Plate VI, Figs. 4,5) D. nuttallii
13. Leaves glabrate to pilose; bracts glabrate or sparsely hairy, ovate-acuminate to subulate, usually narrowed at base; stipules not reddish. (Plate VIII, Figs. 1-3,5)
15. Pedicels mostly 10-20 mm. in length; flowers 8-10 mm. long; leaflets glabrate, glaucous beneath, ovate, (Plate V, Figs. 3-5) D. laevigatum
15. Pedicels mostly 5-10 mm. in length; flowers 5-8 mm. long; leaflets various, not glaucous beneath. (Plate VIII, Figs. 1-5) D. paniculatum

12. Loment segments rounded or angled beneath, 7-10 mm. long; stipules and bracts lanceolate; bracts very conspicuous before anthesis; flowers 8-12 mm. long. (Plate II, Fig. 1; Plate IV, Fig. 6)
16. Loment segments 7-10 mm. long, angled below; petioles of median leaves exceeding 2 cm. in length. (Plate IV, Figs. 5-7). D. cuspidatum
16. Loment segments 5-7 mm. long, rounded below; petioles of median leaves usually less than 1.5 cm. in length. (Plate II, Figs. 1-3) D. canadense

Key to Species of Desmodium - Vegetative Characters

1. Stipels obsolescent; leaves usually subverticillate. (Plate III, Fig. 2)
 2. Terminal leaflet as broad as, or broader than, long, strongly acuminate; leaves usually clustered at base of inflorescence. (Plate III, Figs. 2,3) Desmodium glutinosum
 2. Terminal leaflet as long as or longer than broad, acute or weakly acuminate; leaves clustered at apex of sterile stem or dispersed. (Plate VI, Figs. 2,3)
 3. Leaflets 1.5-1.7 times longer than wide; leaves usually clustered at apex of sterile stem; plants locally abundant. (Plate VI, Figs. 2,3). D. nudiflorum
 3. Leaflets 1-1.4 times longer than broad; leaves dispersed on flowering stem; plants not common. (Plate VII, Figs. 1,2). . D. pauciflorum
1. Stipels persistent; leaves scattered. (Plate II, Fig. 8)
 4. Plants trailing vines. (Plate V, Fig. 6)
 5. Terminal leaflets suborbicular; leaf pubescence of straight or curved trichomes. (Plate IX, Fig. 1) D. rotundifolium
 5. Terminal leaflets ovate; leaf pubescence of predominantly hooked trichomes. (Plate V, Fig. 6). D. ochroleucum
 4. Plants not trailing vines.

6. Blades predominantly pubescent with hooked hairs; stipules conspicuous, ovate-deltoid, usually 3-5 mm. wide, semi-clasping at base. (Plate II, Fig. 8; Plate IV, Fig. 4)
7. Stem branching, the upper portion villous-hirsute; leaflets ovate, commonly more than 8 cm. in length; stipules frequently reflexed at maturity. (Plate II, Figs. 7,8) D. canescens
7. Stem simple, glutinous with short, gland-tipped or hooked hairs; leaflets ovate-lanceolate, usually less than 8 cm. long; stipules not reflexed. (Plate IV, Figs. 1,4) D. illinoense
6. Blades predominantly pubescent with straight or curved hairs; stipules ovate-lanceolate or subulate, 0.5-3.0 mm. wide at base. (Plate II, Figs. 2,3)
8. Medial leaves - the uppermost on young plants - short petioled or sessile (petioles less than 1 cm. in length). (Plate II, Fig. 2)
9. Leaves sessile or with petioles less than 3 mm. long; blades narrowly oblong to linear-lanceolate. (Plate IX, Fig. 3) D. sessilifolium
9. Leaf petioles mostly exceeding 3 mm.; blades various in shape, usually broader than above. (Plate II, Fig. 2)
10. Leaflets usually 2-3 cm. long, elliptic to ovate, obtuse or rounded at apex; stipules not exceeding 5 mm. in length. (Plate II, Fig. 5). . . D. ciliare
10. Leaflets usually 4-8 cm. long, ovate to linear-lanceolate, frequently acute; stipules commonly exceeding 5 mm. (Plate II, Fig. 2)
11. Leaves hairy beneath, the pubescence on main veins usually more copious than on secondary nerves; upper stem blades conspicuously shorter petioled and with narrower leaflets than lower ones; stipules lanceolate, up to 10 mm. long, conspicuous, plants erect, simple or branched towards apex; usually found in open areas, roadsides, prairie remnants. (Plate II, Figs. 2,3) D. canadense

11. Leaves hairy or glabrate beneath; pubescence essentially similar on primary and secondary veins; upper blades gradually shorter petioled than lower ones, leaflets scarcely narrower; stipules subulate, less than 10 mm. in length, inconspicuous; plants erect or spreading, branching, usually found in open, rocky or sandy woods, glades or thickets. (Plate VII, Figs. 1-3, 5). D. paniculatum
8. Medial leaves with petioles exceeding 1 cm. (Plate VIII, Fig. 2)
12. Leaves velvety-pubescent beneath; stipules commonly hairy and reddish in color, ovate-deltoid, broadest slightly above base. (Plate IX, Fig. 5)
13. Terminal leaflets frequently 8-10 cm. in length, more than half as long as wide; plants apparently not extending north of Missouri; not clearly distinguishable from following species by vegetative characters. (Plate IX, Fig. 5) D. viridiflorum
13. Terminal leaflets usually not exceeding 8 cm. in length, about half as wide as long; plants extending north to Indiana. (Plate VI, Fig. 5) . D. nuttallii
12. Leaves glabrate to pilose beneath; stipules various, usually subulate or lanceolate, not becoming reddish. (Plate VIII, Figs. 1-2, 5-6)
14. Terminal leaflet broadly ovate, rounded at apex, not exceeding 3 cm. in length; plants usually glabrate; stipules small. (Plate V, Fig. 1) D. marilandicum
14. Terminal leaflet ovate to lanceolate, acute or somewhat obtuse at apex, usually 4-10 cm. in length; plants and stipules various. (Plate VIII, Figs. 1-2, 5-6)
15. Stipules ovate-lanceolate, 1-2 cm. long; leaflets large, the terminal frequently exceeding 10 cm. in length. (Plate IV, Fig. 5) D. cuspidatum
15. Stipules subulate, usually less than 1 cm. in length; leaflets various. (Plate VIII, Figs. 1-2, 5-6)

16. Leaflets glaucous on lower surface, ovate, sparingly pubescent. (Plate V, Fig. 3)... D. laevigatum
16. Leaflets not glaucous on lower surface, various in shape, commonly hairy. (Plate VIII, Fig. 1-3, 5-6)
17. Terminal leaflet considerably larger than lateral ones, blades appearing thick and rough, distinctly reticulate; petioles not exceeding 2 cm. in length. (Plate VIII, Fig. 6)... D. rigidum
17. Terminal leaflet only slightly larger than lateral ones, hirsute or scantily strigose beneath; blades various, usually appearing thin and smooth, scarcely reticulate. (Plate VIII, Figs. 1-2, 5) . . D. paniculatum

DESMODIUM CANADENSE (L.) DC. (Plate II, Figs. 1-3. Map 4)

Stems clustered, erect, usually simple below inflorescence, pubescent. Stipules conspicuous, lanceolate, up to 10 mm. in length. Leaves crowded, the lower distinctly petioled (petioles 2-3 cm. in length) with broadly ovate leaflets; the middle and upper appearing short-stalked or sessile (petioles 0.5-1.0 cm. long) with elliptic to ovate-lanceolate leaflets; blades to 10 cm in length, finely pilose, especially on main veins beneath. Floral bracts to 10 mm long, conspicuous before anthesis but soon deciduous. Flowers large, 10-12 mm long, red-violet. Loment short-stalked, 3-5 jointed; segments rounded above and below, 5-7 mm long.

Desmodium canadense occurs throughout the north-eastern and central United States and adjacent Canada south to Virginia and central Missouri west to Nebraska and the Dakotas; it extends further into the western Great Plains than any other eastern species of Desmodium. It is usually found along roadsides, in pastures, glades, and prairie remnants. In the western portion of its range, at least, it was undoubtedly originally a prairie species. Flowering usually occurs in July; fruit is matured during August.

Fassett (1939) comments that leaflet form in this species may be quite variable, those of shade plants being thin, broad, and green; those of specimens found in the open usually being narrow, reticulate, and somewhat whitened as in D. illinoense. Schubert (1950) designates Desmodium

canadense as the type of the series Longibracteata. The group is defined to also include D. cuspidatum (Willd.) Loud. See comments under D. canescens concerning species-relationships in the series Stipulata and Longibracteata.

Young (1940) reports a gametic (n) chromosome complement of 11 for this species.

Desmodium canadense is sometimes planted as an ornamental, primarily in borders. On the other hand, the plant is included by Muenscher (1936) in his treatment of weeds of the United States. This author also states that several other species of Desmodium may invade pastures.

DESMODIUM CANESCENS (L.) DC. (Plate II, Figs. 6-8. Map 5)
Stems erect, branched, younger portions conspicuously villous. Stipules commonly exceeding 1.0 cm in length, ovate-acuminate, broad (usually 3-5 mm wide at base) and slightly clasping, usually spreading or reflexed in age. Leaflets large, ovate, rounded at base, acute or acuminate at apex, pubescent (especially on lower surface) with hooked hairs. Inflorescences branched; axes with long villous hairs predominating. Flowers large, circ. 1 cm long, pink or whitish, drying blue-green. Loment large; segments (2) 3-6 in number, 6-11 mm in length, convex above, angled below.

Desmodium canescens is to be found throughout the eastern and central United States, east to New England, south to Florida, west to eastern Nebraska and Texas. It occurs along roadsides, in thickets or cut-over areas, and in open, dry, sterile woodland. It usually flowers and fruits in August - sometimes earlier in the southern part of its range.

Specimens of D. canescens from the western extreme of its range (Oklahoma, Nebraska) frequently have narrower, more strongly reticulate (illinoense-like) leaves and smaller loment segments than is typical for the species. White-flowered plants, as in several other species of Desmodium, have been given a form name, albidum Fern. Especially hairy plants have variously been termed var. hirsutum (Hook.) Robinson or var. villosissimum T. and G. The value of these subspecific categories is questionable.

Schubert (1950), on the basis of similarity of stipules, places Desmodium rotundifolium, D. ochroleucum, D. canescens, and D. illinoense together in the series Stipulata Schub., with D. canescens the type species. This is a plausible grouping although it is somewhat difficult to assess the relative significance of various plant structures in interpreting the phyletic interrelationships of these species. On the basis of loment, leaf, and habit characteristics, the series Stipulata might be held to be a miscellaneous group of species. For instance, the very large, ventrally angled pods of D. canescens do not resemble those of the other species in this group (except possibly D. ochroleucum) but remind one of D. cuspidatum; the leaves and diffuse, branched inflorescences of these two species are also similar. The smaller loment of D. illinoense with their elliptic or rounded joints bear no resemblance to those of D. canescens but suggest D. canadense (Deam, 1940, believes canadense and illinoense

to be "closely allied"). The pods of D. rotundifolium differ from those of the above species, and this plant is further distinguished by its short axillary inflorescences and absence of hooked trichomes on the blades.

Young (1940) reports a somatic 22, and a gametic 11 chromosomes for this species.

DESMODIUM CILIARE (Willd.) DC. (D. obtusum (Muhl.) DC. of authors) (Plate II, Figs. 4, 5. Map 6).

Stems erect or ascending, clustered, pubescent or in age becoming glabrate, stipules subulate, usually persistent. Leaves short-petioled, those on lower portion of stem 0.5 - 1.5 (2.0) cm long, those of the middle and upper stem subsessile to 1.0 cm in length. Leaflets usually elliptic, sometimes ovate, mostly less than 3 cm in length, finely pubescent. Pedicels 5-9 mm long, stiff, flowers 3-4 mm long. Loment typically 2-jointed, somewhat convex above, undulate-incised below, the segments 4-6 mm long, rounded below and above.

Desmodium ciliare extends from southern New England to northern Florida, west to eastern Texas, inland to Missouri to southern Michigan. The species is said also to occur in Mexico, Cuba, and Haiti. It is characteristic (in the United States) of dry, open woodlands in acid soil. Flowering usually takes place in late August or early September, but occasional plants may be found in bloom by the first of August.

Schubert (1950) designates D. ciliare as the type species of the series Pauciarticulata, which is defined as a group of more or less spreading herbs with small bracts and flowers, and few-articulate loment with small or medium-sized articles. The series includes, besides D. ciliare and the species listed above, D. tenuifolium T. and G., D. strictum (Pursh) DC., and D. lineatum DC., all eastern or southeastern plants.

This plant has frequently been known as Desmodium obtusum (Muhl.) DC. (or Meibomia obtusa (Muhl.) Schindl.)¹ on the basis that the Hedysarum obtusum and H. ciliare of Willdenow, name-bringing synonyms, represented the same species, and were described in the same publication, the epithet obtusum having page priority. However, page priority has no validity in the present rules. Further, the identity of Hedysarum obtusum Willd. has never been definitely established; it has variously been believed to be equivalent to D. ciliare (Willd.) DC. and more recently D. rigidum (Ell.) DC. (Schindler, 1926a). Since the Willdenow herbarium, if still existent, is not readily accessible (presumably in Russian hands), this question cannot easily be clarified. It seems best, therefore, to continue the present interpretation, following Blake (1924).

¹ The names above (and others in Willdenow's Species Plantarum) have frequently been attributed to Muhlenberg, on the basis of Willdenow's "Muhlenb. in litt." Presumably the epithets originated with Muhlenberg on herbarium labels or as manuscript names. However, the descriptions are Willdenow's (Willd. Sp. Pl. 3(2):1190 and 1196. 1802).



PLATE II, DESMODIUM

Desmodium canadense, 1. Mature loment x 1-2/3. 2. Leaf and stipule x 2/3. 3. Undersurface of leaf blade showing typical vein and veinlet pubescence x 5. D. ciliare, 4. Mature loment x 2-2/3. 5. Leaf and stipule x 1-1/3. D. canescens, 6. Mature loment x 1-1/3. 7. Portion of inflorescence x 2/3. 8. Leaf and stipule x 2/3.

D. ciliare and D. marilandicum closely resemble one another, and are frequently confused in herbaria. The most distinct differential characters have to do with the pedicels; shorter and more rigid in D. ciliare; the leaves shorter petioled in D. ciliare; and the leaflets elliptic, somewhat thicker, slightly more reticulate and hirsute in D. ciliare. While the vegetative characteristics are somewhat variable, if all are considered simultaneously, one species or the other is usually definitely indicated.

Graham (1941) notes that the seeds of this plant are to be considered an important food for the bobwhite.

The gametic chromosome number of D. ciliare is 11 (Young, 1940 - reported as D. obtusum).

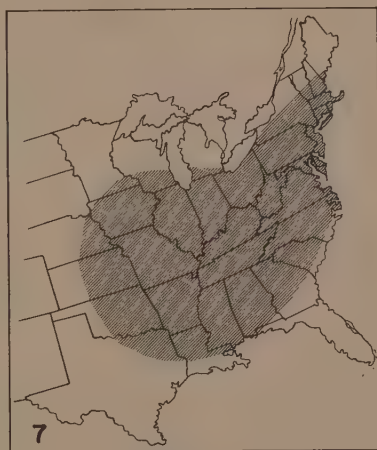
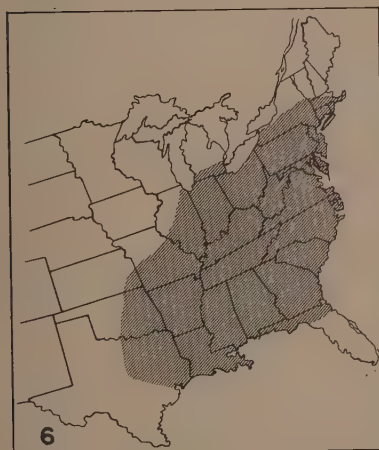
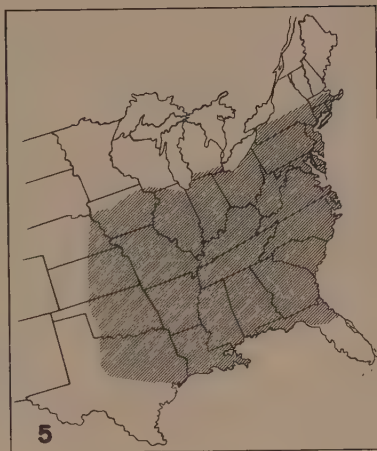
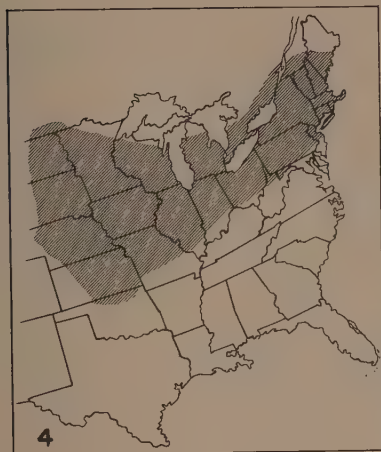
DESMODIUM CUSPIDATUM (Willd.) Loud. (D. grandiflorum (Walt.) DC., not of recent authors; D. bracteosum (Michx.) DC.) (Plate IV, Figs. 5, 7. Map 7)

Stems erect, glabrous or puberulent with hooked hairs. Stipules lanceolate, conspicuous, persistent, 1-2 mm wide at base, frequently exceeding 1 cm in length. Leaves long-petioled. Leaflets large, often over 10 cm in length; ovate to lanceolate-ovate, acute or acuminate-tipped, rounded at base, glabrous, or pubescent, subglaucous beneath. Inflorescence axis closely uncinate-pubescent, rarely with some villous hairs. Floral bracts 5-10 mm long, striate-nerved, conspicuous in budding inflorescences but deciduous. Flowers pink, large, 8-10 mm long when fully expanded. Loments (3) 4-7 jointed; segments 7-11 mm long, curved or nearly straight above, angled below.

Desmodium cuspidatum is distributed throughout most of the eastern half of the United States, extending from southern Minnesota and Wisconsin to New England on the north, west to Nebraska and eastern Texas, and southeast to Florida. In the north-central states it is apparently absent from the Dakotas, the northern portions of Minnesota, Wisconsin, Michigan, and western Nebraska and Kansas. Records from the southeastern states are sporadic; the actual distribution may not be as continuous as indicated on the map.

D. cuspidatum is frequently found in richer or denser woodland than most species of Desmodium, but also occurs in thickets, along roadsides, and in timber openings. Flowering occurs about the first of August.

As Schubert (1950 p. 138) has commented, "there has been considerable changing about of names for this plant..." This author gives a full synonymy and literature citation. Briefly, D. cuspidatum has been known as D. bracteosum (Michx.) DC. (or equivalent in the genus Meibomia) in most literature. Hedysarum bracteosum was published by Michaux in 1803. The name H. cuspidatum, referring to the same plant, appeared in volume 3, part 2, of Willdenow's edition of Species Plantarum, which, as recently demonstrated by Schubert (1942), was apparently printed in 1802; hence the epithet cuspidatum takes precedence. Hedysarum grandiflorum Walt. (Desmodium grandiflorum (Walt.) DC.) again is this same



4. Desmodium canadense. 5. D. canescens. 6. D. ciliare. 7. D. cuspidatum.

plant. Published in 1788, this name is older than either of the above two, but is antedated by the homonym, Hedysarum grandiflorum Pall. 1773.¹

D. cuspidatum is quite well marked, and, as species of Desmodium go, easily recognized. In fruit, characterized by its very large lomenta,

¹ However, the binomial D. grandiflorum as employed in the 7th edition of Gray's manual (Robinson and Fernald, 1908) and other relatively recent American works is a misapplication to D. glutinosum.

it is similar only to D. canescens from which it differs in stipule, leaf, and pubescence characters. Vegetative or early flowering specimens in herbaria are sometimes confused with D. canadense or D. paniculatum var. dillenii. The following characters of D. cuspidatum may be emphasized in distinguishing these species: the large, long-petioled leaves, the conspicuous stipules and (early deciduous) bracts, the closely uncinat (without longer villous hairs) inflorescence axis, and the large flowers.

Most authors have recognized two varieties of this species. These are: variety cuspidatum: stems, leaves and bracts glabrate or puberulent; variety longifolium (T. and G.) Schub. (D. bracteosum longifolium (T. and G.) Robins.; D. longifolium (T. and G.) Smyth): stems and leaves pilose and puberulent; bracts puberulent and pilose-ciliate. These two varieties can usually be distinguished and show some geographical segregation. The typical species extends from eastern Texas, central Illinois, northeast to New England. Var. longifolium is primarily restricted to the central states (extending east only to Ohio) and for the most part represents the species in the northern part of this range.

Young (1940) reports a gametic chromosome number of 11 for D. bracteosum.

DESMODIUM GLUTINOSUM (Willd.) Wood (D. grandiflorum of authors, not (Walt.) DC.; D. acuminatum (Michx.) DC.) (Plate III, Figs. 1-3. Map 8)

Stem erect, simple below inflorescence. Leaves usually subverticillate. Stipules linear, semi-persistent. Leaflets ovate, the terminal one as broad or broader than long and with a conspicuously acuminate apex. Stipels obsolescent. Inflorescence paniculate, terminal above leaf cluster. Pedicels about 5 mm long. Flowers pink, occasionally white; calyx teeth shorter than tube. Loment stalk 4-6 mm long. Loment nearly straight above, incised below with 2-3 somewhat asymmetric segments, 8-9 mm long. Seeds large, thin, about size of loment segments, fragile and easily breaking. Seed coat membranous, brownish.

This plant occurs throughout the eastern United States, with the exception of tropical Florida, west to the eastern Dakotas, south to Texas. It is present in the southern portions of Ontario and Quebec, and Schubert (1950) has recently reported collections from the states, Nuevo Leon, Puebla and San Luis Potosi, in Mexico. Rudd (1951) enumerates D. glutinosum (as D. acuminatum) in eastern North Dakota as one of several examples of eastern deciduous forest species which have invaded this area subsequent to the recession of the late Wisconsin glaciation.

D. glutinosum is relatively common in rich or rocky woodlands, flowering early to mid-summer - usually about the end of June in north-central states but sporadic blooming may take place later. Mature fruits may be found after July 15th.

The taxonomic affinities of D. glutinosum lie with D. nudiflorum and pauciflorum. These three species form a group somewhat distant, phylogenetically speaking, from the other American Desmodia (see page 41).



PLATE III, DESMODIUM

Desmodium glutinosum, 1. Mature loment x 2.
 2. Habit, semi-diagrammatic x 1/2. 3. Leaf x 3/4.
 (55)

These species are relatively constant morphologically, and show no tendency towards intergradation.

Such variability as I have observed in D. glutinosum has been limited to occasional white-flowered forms, and sporadic plants or colonies in which one, several, or all of the leaves are scattered on the stem—rather than being closely clustered as in the typical species. This latter phenotype has been called forma chandonettii (Lunell) Schub. Plants with unifoliate leaves have been termed forma unifoliolatum (Schub.) Schub.

Several years ago, the author planted seeds of D. glutinosum in the greenhouse. The germination was hypogeal (the cotyledons remaining in the ground) a behavior most frequently associated with the Vicieae. In this characteristic, D. glutinosum differs from any other desmodiums or lespedezas whose seedlings I have observed, but is possibly shared by the related species, D. nudiflorum and pauciflorum. All or most of the first year leaves were unifoliate, the blade having the shape of the terminal leaflet of subsequent leaves. On first-year plants observed in the field, as well as on the seedlings grown in the greenhouse, no inflorescence was produced during this initial growing period.

A gametic chromosome number of 11 has been reported (Young, 1940) for D. grandiflorum, presumably referring to this species.

DESMODIUM ILLINOENSE Gray (Plate IV, Figs. 1-4. Map 9)

Stems erect, usually simple, with uncinata and glandular pubescence. Stipules conspicuous, persistent, exceeding 1.0 cm, ovate-acuminate, truncate or semi-clasping at base. Petioles approaching leaflets in length. Leaflets narrowly ovate to ovate-lanceolate, strongly reticulate, acute at apex, somewhat sticky beneath; pubescence of hooked hairs. Inflorescence axis thick, simple or slightly branched, glutinous with jointed glandular hairs. Flowers slender-pedicelled, frequently appearing somewhat whorled, white or pinkish. Loments with 3-6 elliptic or rounded segments, 5-7 mm long.

This plant is an inhabitant of the north-central United States, northeast to southern Michigan, west to southeastern South Dakota and Kansas. Doubtless originally a prairie species, it now occurs along roadsides, in woodland glades, thickets, prairie remnants, usually in sterile, neutral to acid soil. Flowering is usually about the middle of July—somewhat earlier than many other Desmodium species.

A Desmodium which appears most reasonably associated with D. illinoense occurs in east-central Texas. On the basis of material which I have seen, the area occupied by this plant is disjunct from that of D. illinoense, the latter apparently being absent from Oklahoma and Arkansas. Fassett's distributional map of this species (1939, p. 96) also demonstrates this phenomenon. Furthermore, the Texas specimens are at variance with the more northern representatives of the species as regards both leaf and fruit characters. Their relationships deserve further study.

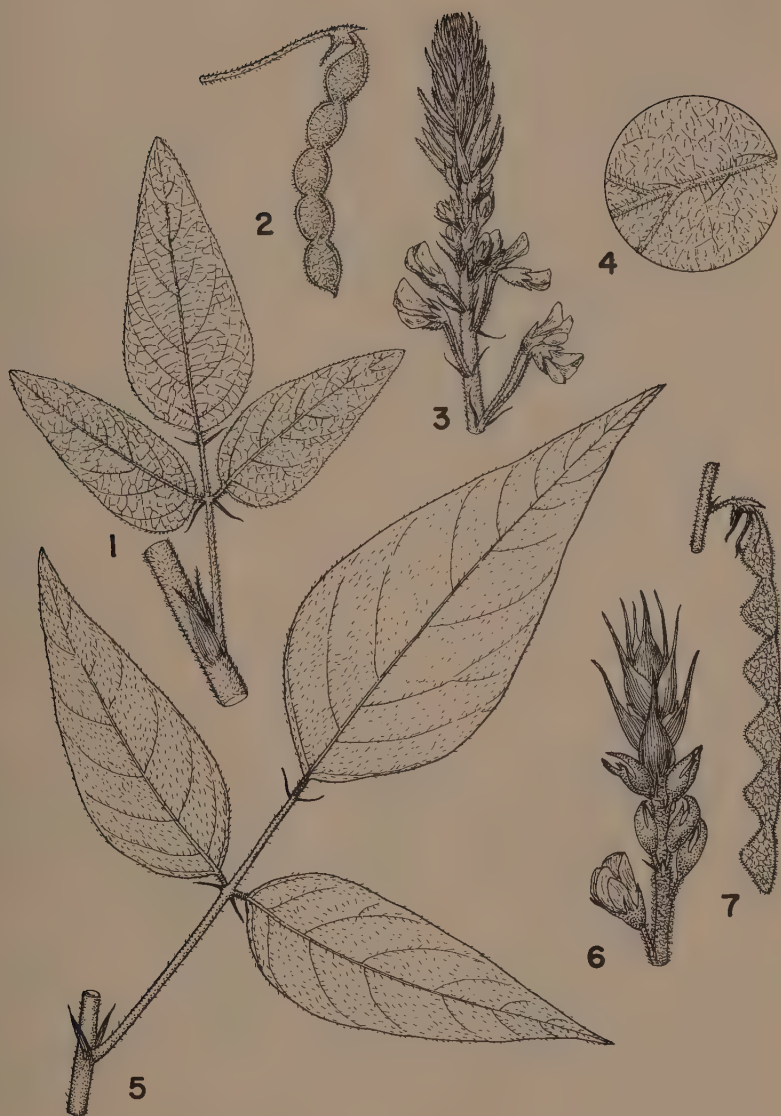


PLATE IV, DESMODIUM

Desmodium illinoense, 1. Leaf and stipule $\times 2/3$. 2. Mature loment $\times 1-1/3$. 3. Inflorescence $\times 2/3$. 4. Undersurface of leaf showing typical pubescence $\times 8$. *D. cuspidatum*, 5. Leaf and stipule $\times 2/3$. 6. Tip of young inflorescence $\times 2$. 7. Mature loment $\times 1$.

DESMODIUM LAEVIGATUM (Nutt.) DC. (Plate V, Figs. 3-5. Map 10)
Stem erect, glabrate. Stipules early deciduous. Leaves strongly petioled. Leaflets ovate, relatively large, glabrous, or puberulent on nerves, glaucous beneath. Flowers pink to lavender, large, 8-10 mm long. Pedicels slender, 10-19 mm long. Loments conspicuously (4-5 mm) stalked above calyx, 3-5 jointed, the segments usually angled above and below, 5-7 mm long.

This species occurs throughout most of the eastern United States south of New England, west to southern Missouri and eastern Texas. It is usually found in scattered stands in open woods and glades, blooming in late August or September.

Young (1940) has tabulated gametic chromosome numbers of 11 for two collections of *D. laevigatum*.

DESMODIUM MARILANDICUM (L.) DC. (Plate V, Figs. 1-2. Map 11)
Stems clustered, usually erect, frequently not branched below inflorescence, scantily puberulent or glabrate. Stipules subulate. Leaf petioles 1.5-2.5 cm long, those of uppermost blades sometimes shorter. Leaflets usually not exceeding 2.4 cm in length, broadly ovate, thin and with obscure venation, glabrate or sparsely pubescent beneath. Pedicels slender, usually exceeding 1 cm, frequently slightly arcuate. Flowers 3-4 mm long. Loments mostly 2-jointed, slightly lunate (convex above), undulate-incised beneath; segments rounded above and below, 4-6 mm long.

From New England, *D. marilandicum* ranges west to central Missouri, south to Georgia and eastern Texas. It is characteristic of open woodlands with acid soil. Deam (1940) indicates that in Indiana it is restricted to black and white oak ridges in poor soil. It flowers in August or September.

A gametic chromosome number of 11 has been determined by Young (1940).

DESMODIUM NUDIFLORUM (L.) DC. (Plate VI, Figs. 1-3. Map 12)
Stems of two kinds, a sterile leaf-bearing shoot and a naked inflorescence. Leafy stems erect, low, unbranched. Leaves borne in an apical cluster (or infrequently scattered). Stipules quickly deciduous. Leaflets elliptic to ovate, 1.5-1.7 times longer than wide, puberulent or glabrate. Fertile scapes one or several, arising as underground branches of leafy stems, becoming 2-3 times taller, scapose, or rarely leaf-bearing. Inflorescence borne on upper portions of fertile axis, racemose or paniculate. Pedicels filiform, 10-20 mm long. Flowers pink or occasionally whitish; calyx teeth inevident. Loment stalk 9-10 mm in length. Loment ventrally incised; segments 2-4 in

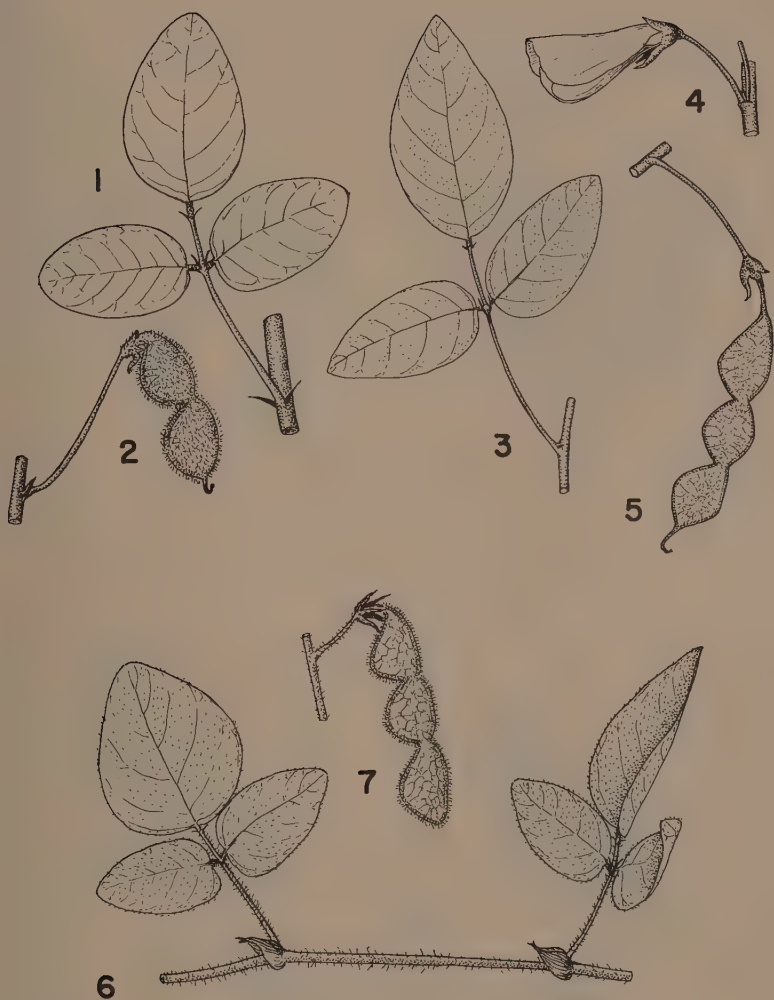
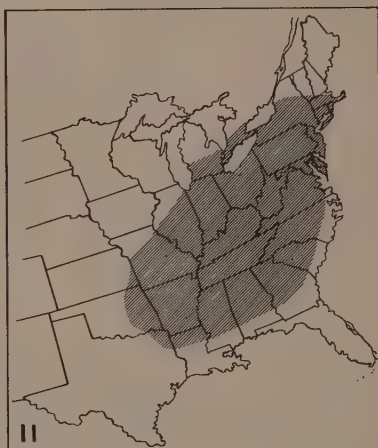
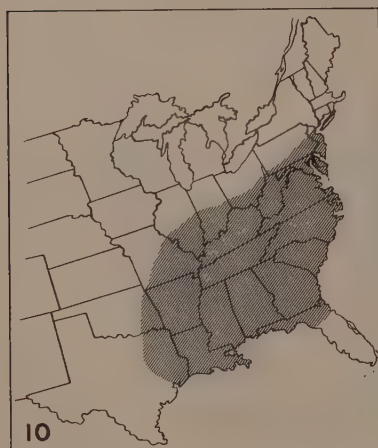
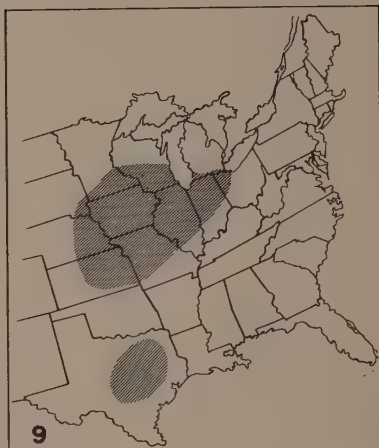
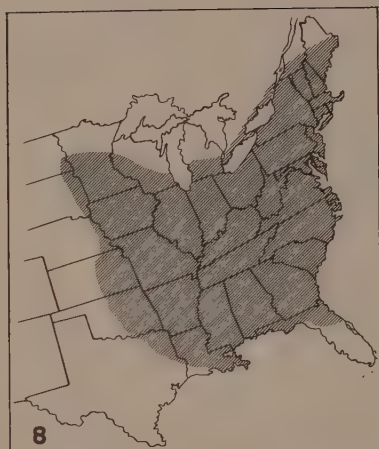


PLATE V. DESMODIUM

Desmodium marilandicum, 1. Leaf and stipule $\times 1-1\frac{1}{3}$. 2. Mature loment $\times 1-2\frac{2}{3}$. *D. laevigatum*, 3. Leaf $\times 1\frac{1}{3}$. 4. Flower $\times 2$. 5. Mature loment $\times 2$. *D. ochroleucum*, 6. Portion of leaf-bearing stem $\times 1\frac{1}{2}$. 7. Loment $\times 1-1\frac{1}{3}$.



8. *Desmodium glutinosum*. 9. *D. illinoense*. 10. *D. laevigatum*.
11. *D. marilandicum*.

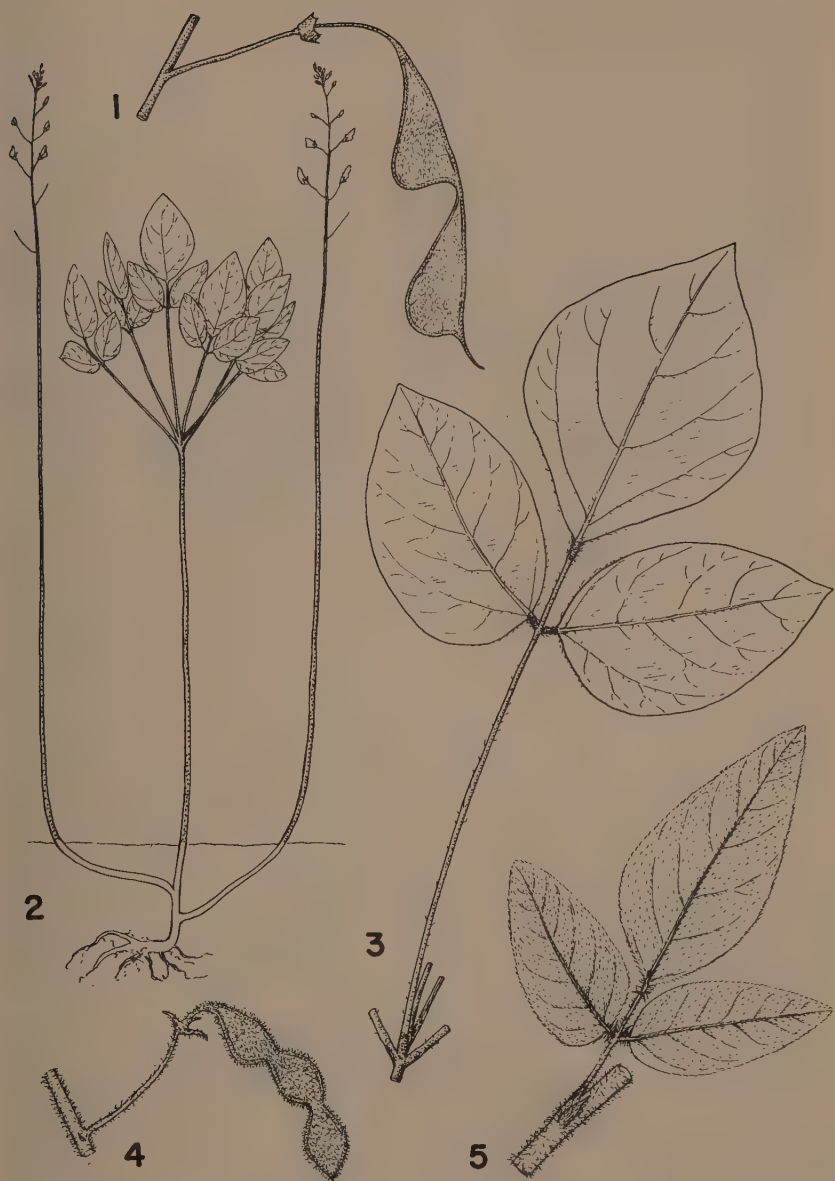


PLATE VI. DESMODIUM

Desmodium nudiflorum. 1. Mature loment $\times 2$. 2. Habit, semi-diagrammatic $\times 2/9$. 3. Leaf $\times 2/3$. *D. nuttallii*, 4. Mature loment $\times 1-2/3$. 5. Leaf and stipule $\times 2/3$.

number, 6-8 mm long. Seeds large, thin and fragile with a reduced seed coat.

This species is characteristic of woodlands in the eastern United States southwest to eastern Texas and adjacent Oklahoma, northwest only to eastern Iowa and Minnesota, northeast to southern Maine and adjacent Quebec. It does not occur in peninsular Florida. Fassett (1939) states that in Wisconsin it is almost invariably found in association with D. glutinosum; the present author has made similar observations in the southeastern states. Deam (1940) believes it to be most frequent in Indiana in black and white oak woodlands. Flowering usually occurs in June and July; fruits are mature about a month later.

Like its relatives (D. glutinosum and D. pauciflorum), D. nudiflorum is a clear-cut species. It is relatively constant throughout its range except for occasional variants in leaf arrangement and flower color, i.e.: leaves on the flowering stem (formae foliolatum (Farw.) Fassett and personatum Fassett) flowers white, (forma dudleyi (House) Fassett).

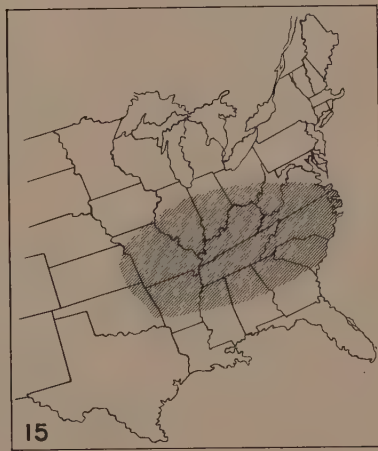
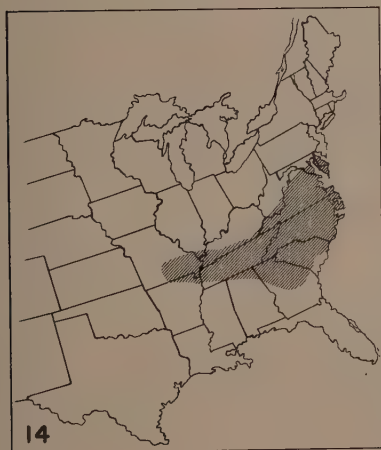
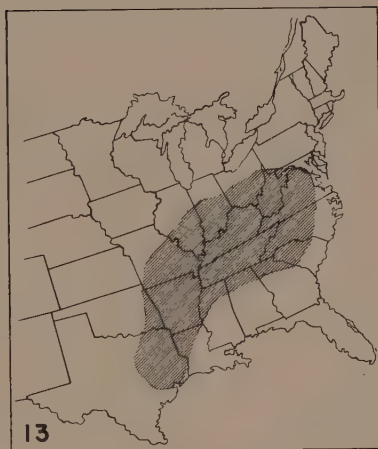
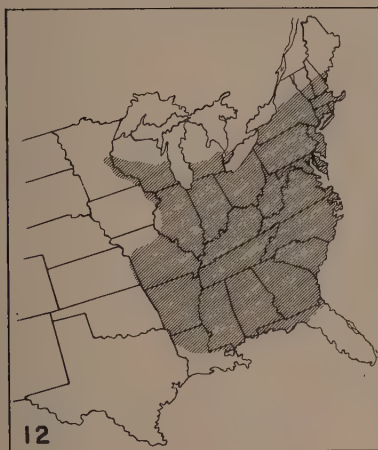
The gametic chromosome number of D. nudiflorum, as reported by Young (1940), is 11.

DESMODIUM NUTTALLII (Schindl.) Schub. (D. viridiflorum of authors in part) (Plate VI, Figs. 4, 5. Map 13)

Stems erect, pubescent. Stipules deltoid-ovate, puberulent, frequently reddish. Leaflets ovate to elliptic, rarely exceeding 10 cm, velvety or tomentose beneath. Bracts deltoid, hairy. Flowers lavender, turning greenish-blue in age, with relatively short pedicels (4-5 mm), lomenta distinctly stalked, usually 3-, sometimes 4-jointed, curving inwards, i.e., the upper margin convex, the lower, concave; segments mostly 3.5-5.0 mm in length, usually rounded above and below.

This species occurs primarily in the eastern and southern United States. In the north-central states area it appears to be limited to Missouri, southern Illinois and Indiana. My collections of the plant have all been in open woodland on steep slopes or at the top of hills. Flowering: August, September; fruiting: September, October; plants from southern Texas may bloom considerably earlier.

D. nuttallii is essentially similar in general appearance to D. viridiflorum, to which it is closely related. Its elaboration, as a previously unrecognized entity in the D. viridiflorum complex has been relatively recent (Schindler, 1926a), the diagnosis being based primarily upon differential shape of loment segments. However, little cognizance was taken of the species in American literature until Schubert (1950, 1950a) reiterated Schindler's conclusions and in addition pointed out that D. nuttallii averaged the smaller in most plant parts, especially that it possessed smaller, nearly elliptic leaflets, broadest about the middle. The leaflets of D. viridiflorum were said to be the larger (the terminal 5.2-11.8 cm long), ovate to deltoid, broadest below middle and frequently two-thirds as wide as long. Schubert also indicated that D. viridiflorum was primarily a coastal plain species extending "inland only to Arkansas and Tennessee,"



12. Desmodium nudiflorum. 13. D. nuttallii. 14. D. ochroleucum.
15. D. pauciflorum.

whereas D. nuttallii was more widespread in the central part of the country. The problem was reinvestigated by Isely (1954) who employed measurement data to determine the practicability of distinguishing these closely related entities. His conclusions were essentially in agreement with those of previous authors. However, while calling attention to several additional differential loment characters, he indicated that generalizations in regard to leaflet size and shape (while apparently valid as averages for the species) needed to be applied with extreme caution in the identification of individual specimens; hence, the species are difficult to differentiate in vegetative condition. His data did not indicate the ranges of these species to be as distinct as previously reported.

Due to the rather recent recognition of D. nuttallii in American botanical literature, Fernald's Manual of Botany (1950) is the only floristic treatment covering the north-central states which includes this species. It is reported in other treatments as D. viridiflorum.

DESMODIUM OCHROLEUCUM Curtis (Plate V, Figs. 6, 7. Map 14)
Plant prostrate, except for ascending racemes. Stem pubescent with villous and hooked hairs. Stipules ovate-acuminate, somewhat clasping, reflexed in age. Leaflets ovate, strongly reticulate and with hooked hairs below. Racemes axillary and terminal, villous pubescent. Flowers white¹. Loments 3-4 jointed, the margin frequently appearing twisted; segments elliptic, 7-9 mm long.

D. ochroleucum is an uncommon eastern species ranging north to Delaware, south to Georgia, (reported from Florida) and west to south-eastern Missouri. It flowers and fruits in August and September.

Vegetatively, this plant is almost identical with D. canescens except for the difference in habit. It is possible that its closest relationships may be with that species rather than the decumbent D. rotundifolium with which it usually associated.

DESMODIUM PANICULATUM (L.) DC. (Incl. D. dillenii Darl; D. perplexum Schub; D. glabellum (Michx.) DC.) (Plate VIII, Figs. 1-5. Map 16)
Stems erect or ascending, usually with spreading branches, glabrate, uncinat-puberulent, to moderately villous. Stipules subulate, early deciduous or semipersistent. Leaves long or short-petioled. Leaflets variable as to shape and pubescence, frequently narrow (oblong to lanceolate) with sparse, appressed pubescence, or, alternatively, ovate with spreading pilosity. Flowers 5-8 mm long. Loments 3-5 jointed, the segments usually slightly curved above, angled or obtusely rounded beneath.

¹I have never collected this species, hence have not verified flower color from living specimens. A specimen collected by Dr. Fernald bears the following notation: "Corolla bright white; standard with a green spot; keel petals pink tipped."

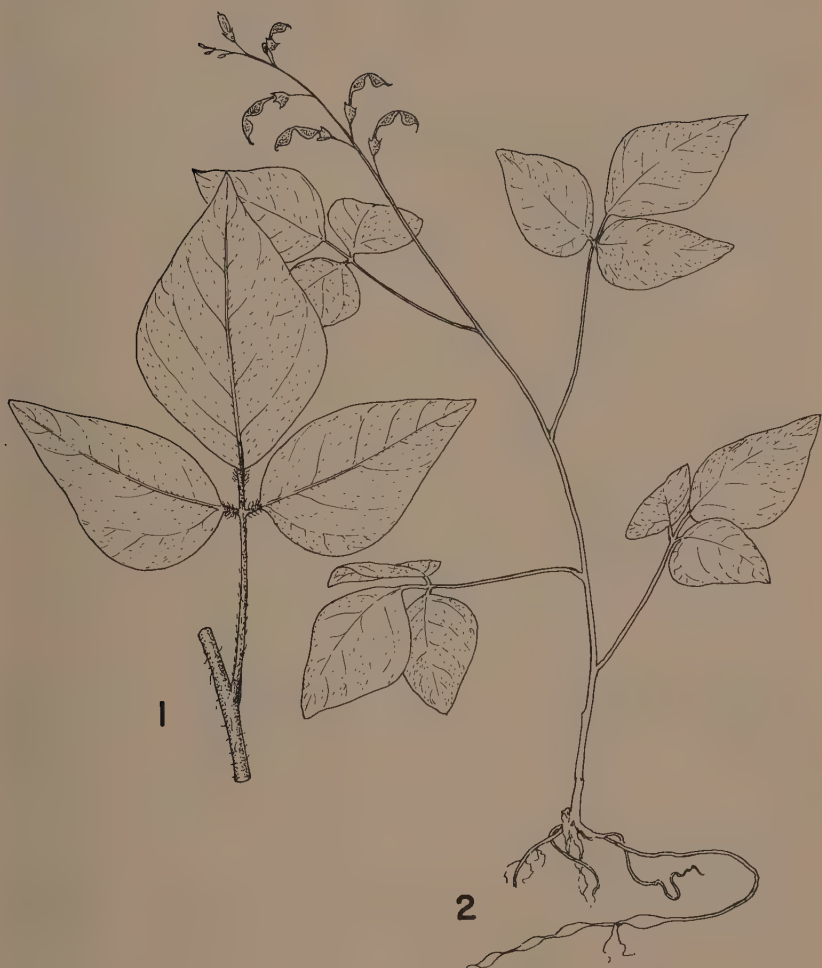


PLATE VII. DESMODIUM
Desmodium pauciflorum, 1. Leaf $\times 2/3$. 2. Habit $\times 1/3$
(65)

D. paniculatum occurs throughout the eastern United States, exclusive of peninsular Florida, west to central Texas and eastern Nebraska. Its distribution in the north-central states area excludes the Dakotas and Minnesota, western Nebraska and Kansas, and northern Wisconsin and Michigan. However, it is possibly the most abundant Desmodium in the central and south-central United States in open or dense woodlands and along roadsides. It usually flowers in August or early September.

Petal color in this species is quite variable, ranging from lavender, blue- or greenish-lavender, to red-purple, or rarely white. To some extent, this color range is due to changes as the flowers age or wilt, usually proceeding from a brighter red or purplish hue to a duller blue-green. The flowers of several other species also appear green when dried. The loment stalks are variable in length (usually 2-4 mm), and average shorter than those in either of the related species D. viridiflorum or laevigatum. The segments are quite consistent in shape but may vary considerably in size; at least part of this variability seems to be correlated with degree of maturity and the number of segments maturing per loment (larger segments on those with few joints).

Desmodium paniculatum represents a complex which is extremely variable as regards leaflet shape and pubescence. The extremes are quite unlike in appearance and the group has been regarded as constituting 2-5 species by all previous authors, except Schindler (1926). In many local areas two or more phenotypes not only appear distinct but occupy different habitats. However, the complex was recently investigated by the present author (Isely, 1954) who concluded that it was most satisfactorily treated as a single species because: (1) fruit characters were relatively consistent, (2) variation in leaflet shape and pubescence was essentially quantitative; there was no consistent nor practical manner in which the series of variants could be broken into mutually exclusive groups. Isely (l.c.) recognized two varieties as a means of describing the most common contrasting forms. These are as follows:

Desmodium paniculatum (L.) DC. var. paniculatum. (Including Desmodium paniculatum (L.) DC., Meibomia chapmani (Britt.) Small, M. angustifolia (T. and G.) Kearney of various manuals.) Terminal leaflets usually 3-8 times as long as broad. Leaflet pubescence moderate to scant, commonly appressed. Stems glabrate or uncinat-puberulent. This variety apparently extends throughout total range of the species and intergrades in various manners with the following.

Desmodium paniculatum var. dillenii (Darl.) Isely. (Including, at least in part, Desmodium dillenii Darl., D. perplexum Schub., D. paniculatum var. pubens T. and G. of various manuals.) Terminal leaflets mostly 1.5-2.5 (3) times as long as wide. Lower surface of leaflets pubescent, predominantly with spreading trichomes. Stems pubescent, usually with a mixture of hooked and spreading hairs.

All combinations of leaflet and pubescent characters blend with the above extremes in more-or-less continuous series, e.g.: (1) hairy plants with narrow leaflets, (2) hairy plants with moderately narrow leaflets, (3) plants with small or large leaflets with limited pubescence, (4) plants with moderately broad or somewhat narrow leaflets with scant pubescence, (5) plants with broad, small, thin, glabrate leaflets.

On the basis of the study cited above, and subsequent examination of

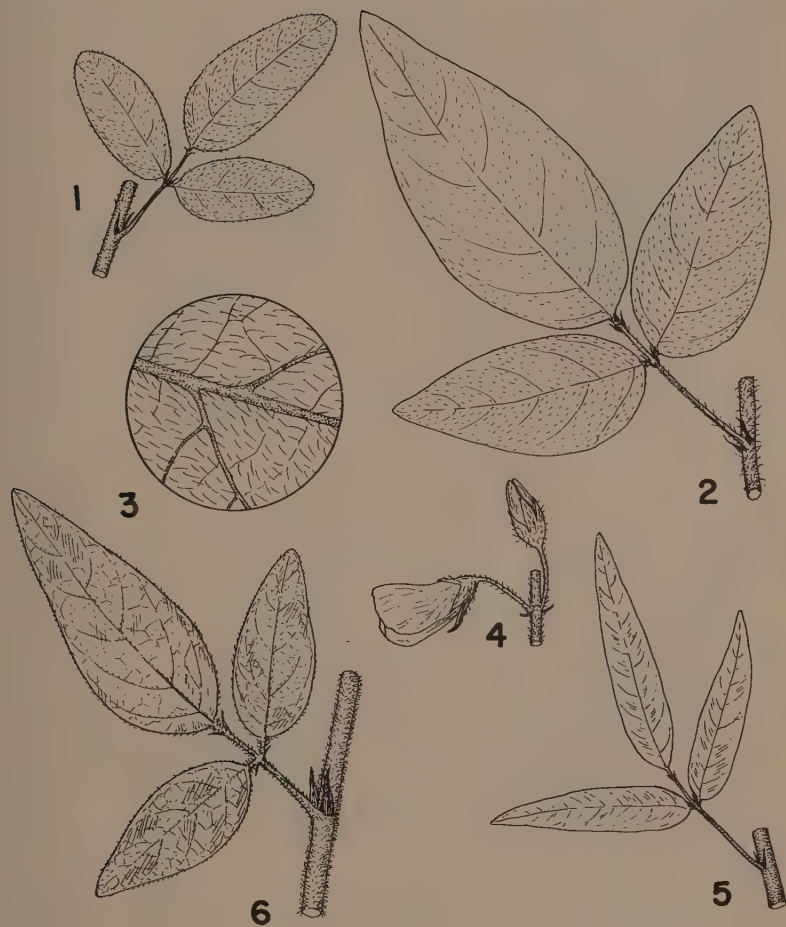


PLATE VIII. DESMODIUM

Desmodium paniculatum, 1. Leaf, pubescent with round-tipped leaflets $\times 2/3$. 2. Leaf with large leaflets, moderately pubescent, somewhat pointed at tip $\times 2/3$. 3. Undersurface of leaflet to show vein and veinlet pubescence $\times 4$. 5. Flowers $\times 2$. 5. Leaf with narrow leaflets $\times 2/3$. D. rigidum, 6. Leaf and stipule $\times 2/3$.

approximately 1000 additional specimens, it appears that, for the most part, all of these phenotypes extend throughout the entire range of the species. The extremes represented by varieties paniculatum and dillenii are possibly more distinct from one another (fewer intermediates) in the northern and eastern states than to the west and the south.

Graham (1941) states that seeds of D. dillenii are considered to be an important food of the bobwhite.

Young (1940) has reported a gametic chromosome number of 11 for both D. dillenii and D. paniculatum.

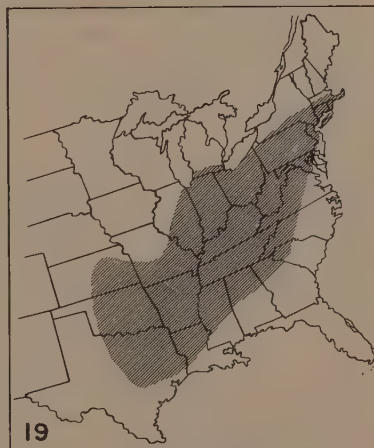
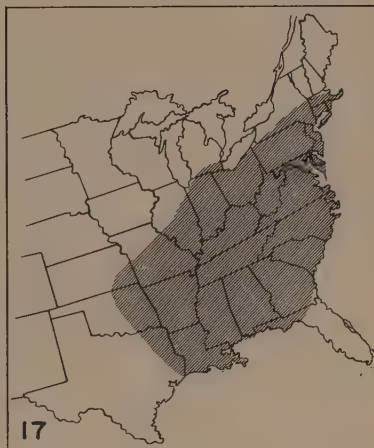
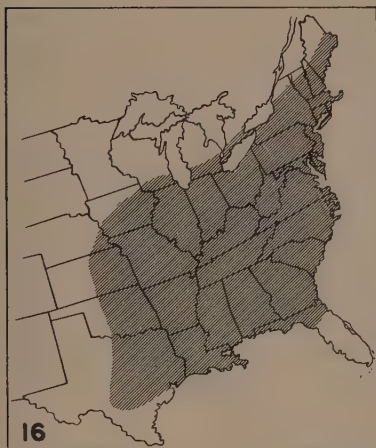
DESMODIUM PAUCIFLORUM (Nutt.) DC. (Plate VII, Figs. 1, 2. Map 15)
Stem ascending or spreading, branched or nearly simple, inconspicuously hairy. Stipules early deciduous. leaflets obovate to rhombic, cuneate at base, short-acuminate at apex, slightly longer than wide, sparsely hairy, frequently whitened on lower surface. Flowers borne in short axillary and terminal racemes, frequently partially hidden by leaves. Pedicels about 5 mm long, frequently recurved. Calyx very short-toothed. Petals white. Loments ventrally incised, borne on stalks 4-6 mm long; segments mostly 1-2, 9-11 mm long.

Rare or occasional in the eastern United States, this species occurs in woodlands from southern Missouri to central New York, southeast to Georgia and north Florida, west to eastern Texas. Deam (1940) states that in Indiana, it is ordinarily found in beech woodland. It usually flowers in the latter part of July or August.

DESMODIUM RIGIDUM (Ell.) DC. (Plate VIII, Fig. 6. Map 17)
Stems clustered, erect, puberulent. Stipules lanceolate, conspicuous on young stems but early deciduous. Leaves short-petioled. Leaflets ovate to lanceolate, rounded at base, obtuse to pointed at apex, reticulate, rough above, hirsute beneath; terminal blades frequently considerably larger than lateral ones, up to 7.5 cm in length. Racemes simple or compound. Floral bracts crowded, conspicuous before anthesis. Pedicels slender, commonly somewhat arcuate. Flowers pink or white, drying yellowish-green, 4-6 mm long. Loments 2-3 (4) jointed, the segments rounded above and below, 4-5 mm long.

D. rigidum is a south-central and eastern species, extending west to eastern Texas. In the north-central states area, it occurs southeast of a line from central Missouri to southern Michigan. It is usually found in open woodlands, fields or prairie areas, generally in acid, sandy soil.

Small-leaved specimens of D. rigidum may resemble D. ciliare. The species may be distinguished - in addition to leaflet size and shape - by the more reticulate leaflets, the more conspicuous stipules and bracts, the longer pedicels, and the greater tendency towards 3- or even 4-segmented loments of D. rigidum.



16. Desmodium paniculatum. 17. D. rigidum. 18. D. rotundifolium.
19. D. sessilifolium.

Schindler (1926) refers this species to Meibomia obtusa (Muhl.) Schindl.,¹ based on Hedysarum obtusum Muhl. ex Willd. The basis for his conclusion is not obvious, although it may be derived from examination of Willdenow's specimens. The original diagnosis (Willdenow, Sp. Pl. 3(2):1190. 1802) could refer to either species; the present status of

¹Nomenclatorially equivalent to the earlier Meibomia obtusa (Muhl.) Vail (1892) although the authors had different plants in mind.

the Willdenow herbarium (presumably in Russian hands) is unknown. In the absence of any definite evidence, it appears desirable, therefore, to employ the currently accepted name.

Young (1940) has indicated the gametic chromosome number of this species to be 11.

DESMODIUM ROTUNDIFOLIUM (Michx.) DC. (*Meibomia michauxii* Vail) (Plate IX, Fig. 1. Map 18).

Stems branched at base, trailing and vine-like in appearance, pilose, or glabrate. Stipules conspicuous, broad and semi-clasping at base, to 1.0 cm long, persistent and becoming reflexed. Leaflets suborbicular, slightly hairy. Racemes primarily axillary, often elongate, 3-9 flowered towards apex. Petals lavender-purple. Loment segments 4-6 in number, elliptic or somewhat angled, 5-7 mm long.

The range of this species is essentially the eastern half of the United States, except for peninsular Florida, west to Missouri and eastern Texas. It is locally abundant in acid soil in open woodlands, usually flowering in August or early September. Deam (1940) states that in Indiana the species occurs in association with black and chestnut oak in clay or sandy soil, and that it is rare except in nonglaciated areas.

Glabrate forms have been termed forma *glabratum* (Gray) Schub. I have seen specimens in which the main stem is hairy, and the branches glabrous.

A gametic chromosome number of 11 has been reported for *Desmodium rotundifolium* (Young, 1940).

Observations in Missouri (Graham, 1941) have indicated the flowers and fruit of the plant to be a preferred food of the eastern turkey.

DESMODIUM SESSILIFOLIUM (Torr.) T. and G. (Plate IX, Figs. 2, 3. Map 19)

Stem erect or ascending, puberulent. Stipules subulate. Leaves sessile or very short petioled. Leaflets narrowly elliptic to oblong-lanceolate, rounded at base and apex, somewhat reticulate, moderately pilose beneath. Pedicels short, less than 5 mm long. Flowers pale lavender, drying blue-green, small. Loment usually 2-3 jointed, the segments 4-6 mm long, rounded both above and below.

This distinctive species is primarily an inhabitant of the eastern and southern states. It ranges north to Massachusetts and southern Michigan, west to central Texas, southeast to South Carolina and Alabama. It is usually found in dry, sandy or sterile soil. In the northern part of its range it appears partial to open areas, but in the southeast is frequent in pine woodlands. Flowering usually takes place in August or September, but in Texas I have found the plant in bud as early as May 26.

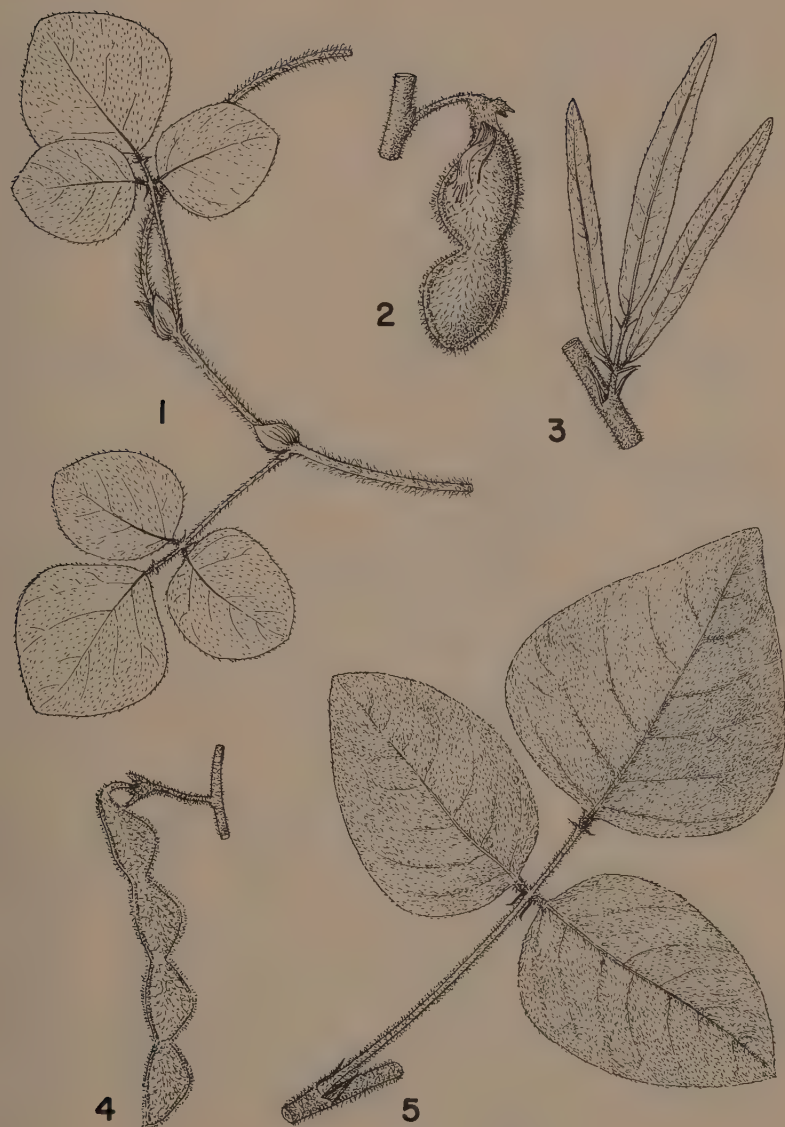


PLATE IX. DESMODIUM

Desmodium rotundifolium, 1. Habit, leaves and stipules $\times 2/3$.

D. sessilifolium, 2. Mature loment $\times 3$. 3. Leaf and stipule $\times 2/3$.

D. viridiflorum, 4. Mature loment $\times 1-2/3$. 5. Leaf and stipules $\times 2/3$.

DESMODIUM VIRIDIFLORUM (L.) DC (Plate IX, Figs. 4, 5. Map 20)

Stem erect, usually simple below inflorescence, pubescent. Stipules deltoid-ovate, puberulent, frequently reddish. Leaves distinctly petioled. Leaflets broadly ovate, the terminal one commonly exceeding 10 cm in length, velvety-pubescent beneath, hirsute or becoming glabrate above. Bracts deltoid, puberulent. Flowers pink, turning blue-green in age, short pedicelled. Loment stalked 3-5 mm above calyx, usually 4-5 jointed, nearly straight, the segments 5-7 (8) mm in length, usually angled below, curved or slightly angled above.

D. viridiflorum occurs in the south-central and eastern states, north to Missouri and west to Oklahoma; it is, for the most part, restricted to the coastal plain. This species has been reported from several states in the north-central area, but these reports are based primarily upon collections of the closely related D. nuttallii.

Schubert (1950) designates D. viridiflorum as the type species of the series Stipitata. The section is defined as possessing primary bracts and flowers which are smaller than those in the Longibracteata (typified by D. canadense), and with longer stalked loment. The species involved (as listed by Schubert) include D. viridiflorum, D. nuttallii (Schindl.) Schub., D. fernaldii Schub., D. paniculatum (L.) DC., D. glabellum (Michx.) DC., D. perplexum Schub. (these latter two names submerged in synonymy under D. paniculatum in present paper), D. humifusum (Muhl.) Beck, D. laevigatum (Nutt.) DC., and D. floridanum Chapm. These species are certainly closely related. Some of them are quite polymorphic (especially in regard to leaflet shape and pubescence) and are not always clearly definable, one from another. Possibly the group is in an early stage of evolution.

D. viridiflorum and nuttallii are closely allied, the latter having been recognized as a distinct entity only within the past few years. The two are discussed on a comparative basis under D. nuttallii. The D. paniculatum and D. floridanum complexes are very distinct from D. viridiflorum in their extreme phases, but individual intermediate specimens may be distinguished from D. viridiflorum only with difficulty. Hairy, broad-leaved extremes of the ubiquitous D. paniculatum group (var. dillenii—see treatment of D. paniculatum) in particular are confounded with D. viridiflorum and nuttallii in herbaria, especially if specimens of the latter represent the less pubescent phases, if much of the pubescence has been lost, or if well developed fruits are not present. In such cases, the shape of the bracts and stipules, if discernible, has been found to be quite helpful. Those of D. viridiflorum and nuttallii are typically deltoid, broadest at or very close to the base, 1.5-2.5 times as long as wide, and not long-acuminate at apex. Those of the D. paniculatum group are usually subulate to ovate-acuminate or awn-tipped.

Young (1940) reports a gametic chromosome number of 11 for D. viridiflorum. His material might have been D. nuttallii.



PLATE X. HEDYSARUM

Hedysarum alpinum, 1. Flower $\times 2\text{-}2/3$. 2. Leaf and stipule $\times 2/3$.
 3. Mature loment $\times 2$. *H. boreale*, 4. Flower $\times 2\text{-}2/3$. 5. Leaf and
 stipule $\times 2/3$. 6. Mature loment $\times 2$.

HEDYSARUM L.

Plants perennial. Leaves odd-pinnate; leaflets subsessile, finely glandular-dotted. Flowers in axillary racemes, usually white or purplish. Calyx regular, 5-toothed. Stamens diadelphous. Loment several-jointed, the flat segments frequently winged, elliptic in face view, connected by medial isthmi.

Hedysarum is said to comprise approximately 80 species of north temperate Eurasia and North America. Several species are boreal, circumpolar plants which occur further south only at higher altitudes. The United States distribution of some six species is primarily limited to the western cordillera and adjacent high plains, and northern New England. Two species are found in the western Dakotas.

Literature

Rollins (1940). North American spp.

Key to Species of Hedysarum

1. Calyx teeth deltoid, shorter than the tube; loment reticulations about as wide as long; leaflets distinctly nerved. (Plate X, Figs. 1-3) H. alpinum
1. Calyx teeth lanceolate to subulate, exceeding tube; loment reticulations laterally elongate, giving the segments a cross-ribbed appearance; leaflets weakly-nerved. (Plate X, Figs. 4-6) H. boreale

HEDYSARUM ALPINUM L. (H. boreale of authors, not Nutt; including H. americanum (Michx.) Britt. and H. philoscia Nels.) (Plate X, Figs. 1-3. Map 3)

Plants perennial. Stems clustered, ascending, glabrate or finely strigose. Stipules brown, adnate at base, to 1.5 cm in length. Leaves petioled. Leaflets 15-23, ovate to oblong-lanceolate. Flowers pink to purple, 1.4-1.8 cm long. Calyx teeth unequal in length, shorter than tube. Wings long-auriculate. Loments (2) 3-5 jointed, the segments 5-7 mm in length, rounded or elliptic, glabrate or puberulent; reticulations about as wide as long.

H. alpinum, according to current concepts, is a wide-ranging boreal species occurring in both Eurasia and North America. It extends south into the United States in two widely separated areas, northern new England, Wyoming and South Dakota. In the latter state, it is apparently restricted to the Black Hills, according to Over (1932) being found in "deep woods at high altitudes."

Rollins (1940) considers the North American representatives of this species to consist of three varieties. Variety americanum Michx. ex Pursh (H. americanum (Michx.) Britt., H. boreale of authors) occurs throughout much of Canada, and is the form found in New England. Var. philoscia (Nels.) Rollins (H. philoscia Nels.) is said to differ in possessing pubescent loments; it is restricted to southern Saskatchewan and Alberta, south to eastern Wyoming and western South Dakota. Var. grandiflora Rollins with slightly larger flowers is found only in Canada.

The present author has encountered difficulty in interpreting H. alpinum var. philoscia. Loments of Wyoming and South Dakota specimens are variable as to size and shape of the segments, and appear to blend with

those of H. occidentale Greene, a more southwesternly distributed species. Large-podded forms appearing about as close to H. occidentale as to H. alpinum are doubtless the basis of Over's (1932) report of H. marginatum Greene (H. occidentale) from South Dakota.

This southern extension of Hedysarum alpinum in western North America is on the eastern side of the cordillera. H. occidentale, differing from H. alpinum primarily in its larger loment segments, lies to the south on the western side of the continental divide. Although probably of northern origin from the H. alpinum plexus, H. occidentale occupies an area almost entirely separate from that of H. alpinum, except for the (possibly more recent) southern montane extension of the latter. Here, the two may have mingled, and local populations, feeling the introgressive efforts of both species, are not clearly identifiable with either. Specimens appearing intermediate in nature have been treated as H. alpinum in the present investigations; further studies may suggest a more practical interpretation.

H. alpinum and H. boreale Nutt. have been much confused with one another. The reader is referred to Rollins (l.c.) for detailed synonymy and discussion.

HEDYSARUM BOREALE Nutt. (Incl. H. pabulare Nels., H. cinerascens Rydb., H. utahense Rydb.; not H. boreale of Robinson and Fernald (1908) and other American authors) (Plate X, Figs. 4-6. Map 3)

Stems clustered, erect, pubescent or glabrate. Stipules conspicuous, broadly lanceolate or deltoid, marginally connate. Leaves petiolate, leaflets 9-15, oblong to elliptic, pubescent to glabrate, glandular-dotted above; venation scarcely discernible. Flowers about 1.5 cm in length, in axillary racemes, usually reddish. Calyx puberulent, the teeth subequal, longer than tube. Loment strigose, 3-4 jointed. Segments suborbicular, not winged, reticulate, the interspaces laterally elongate.

H. boreale extends south from Saskatchewan in the western cordillera and adjacent plains to Utah and Oklahoma. In the north-central states, it is recorded from North Dakota by Rollins (1940) and Stevens (1950), and I have seen specimens from that state. It is reported from South Dakota by Over (1932),¹ and Rydberg (1932), but with reference to H. alpinum.

The habitat requirements of H. boreale appear to be rather plastic. In the eastern portion of its range, it is usually associated with grassland or prairie areas; further west it is encountered on sagebrush slopes or plains; in the mountains it grows in open grassland or oak-pine woodlands, on shale or slate slopes, frequently in gravelly or sandy soil.

Rollins (1940) has clarified nomenclatural and taxonomic confusion surrounding H. boreale. Previous to his study, the name H. boreale was variously applied, usually to one of the varieties of H. alpinum. Also, various phases of this species (H. boreale) have, in most earlier treat-

¹I have examined the South Dakota material through the kindness of Dr. J. M. Winter, curator of the herbarium, University of South Dakota.

ments, passed under separate specific names, i.e., H. pabulare Nels., H. cinerascens Rydb., and H. utahense Rydb. I heartily concur with Rollins' treatment of these as a single species.

H. boreale is conspicuously variable with respect to flower size, pubescence, and leaflet shape. Rollins (1940) recognizes 4 varieties, the characterizations of which may be summarized as follows:

Var. typicum (var. boreale of present rules of nomenclature). Leaflets ovate to oblong, glabrate above, 10-15 (20) mm long; leaves of moderate size, 12-16 mm long; loment not tuberculate over seed. Incl. H. pabulare Nels. and H. carnosulum Greene. Distributed throughout range of species.

Var. cinerascens (Rydb.) Rollins. As above, but leaflets oblong to broadly linear, silvery pubescent on both sides; fruit segments frequently with short tubercles. Widely distributed, perhaps more common in northern portion of area. Incl. H. cinerascens Rydb.

Var. obovatum Rollins. Similar to var. cinerascens but with obovate leaflets, and shaggy spreading pubescence. Described from Nevada.

Var. utahense (Rydb.) Rollins. Leaflets large 15-25 (30) mm long. Presumably localized in Utah. H. utahense Rydb.

The present author's experience with this genus is too limited to allow a proper evaluation of these varietal categories. On the basis of material examined, he is, however, under the tentative impression that the variable characters may occur in nearly all possible combinations and that the varieties as described include certain overlapping phenotypic groups and omit others. A number of specimens were observed which appeared variously intermediate between varieties cinerascens and boreale.

LESPEDEZA Michx. Lespedeza, Bush Clover

Plants predominately perennial herbs or low shrubs; our species herbaceous. Stipules subulate, inconspicuous, except in annual species. Leaflets pinnately trifoliate, without stipels. Flowers of two kinds: petal-bearing and apetalous. Petaliferous flowers conspicuous, pedunculate or subsessile, densely glomerate or in loosely flowered axillary racemes. Apetalous flowers cleistogamous, usually in inconspicuous, axillary clusters. Calyces toothed or cleft, those of apetalous flowers reduced. Corolla purplish or white, or yellowish-white. Stamens diadelphous. Pod (loment) with a single, one-seeded, indehiscent joint, lenticular or flattened, ovate-acuminate.

Lespedeza, containing upwards of 120 species, is native to eastern North America, temperate eastern Asia and Australia. The majority of the species are Asiatic, the North American representatives numbering about fifteen. Of these, twelve native and three introduced species are found in the north-central states.

Lespedeza is related to the polymorphous genus Desmodium and can perhaps be regarded as derived from it through reduction in number of loment joints.

Classical interpretations of the genus (Lespedeza) considered it to contain three subgenera, Campylotropis, Microlespedeza, and Lespedeza. Schindler (1912, 1912a, 1913), the only student who has considered the genus on a world-wide basis during the last 75 years, elevated all three of these subordinate groups to generic rank. His Campylotropis, containing 23 Asiatic species, none of them naturalized in the United States, has been accepted by several subsequent authors. The subgenus Microlespedeza including only the two Asiatic annual species, Lespedeza striata (Thunb.) H. and A. and L. stipulacea Maxim., became Schindler's Krummerowia. The basis of his distinction between Krummerowia and Lespedeza included differential floral and branching characteristics as well as the annual habit of the former; however, this interpretation has been accepted by relatively few authors. Schindler's Lespedeza proper contained 2 sections: Macrolespedeza, Asiatic species without apetalous flowers, and Eulespedeza, American and Asiatic species with apetalous as well as petaliferous flowers.

The occurrence and seed producing potentialities of petaliferous and apetalous flowers of the American species of Lespedeza have not been well understood. In general, the petaliferous flowers are produced in conspicuous inflorescences and the apetalous cleistogamous ones are borne separately in axillary clusters, or mixed with the petal-bearing flowers. A number of authors, following the conclusions of Torrey and Gray (1840), divide the American lespedezas into two groups characterized approximately as follows: (1) flowers yellowish-white, all petaliferous, fertile and seed producing, including Lespedeza capitata, leptostachya and hirta; (2) flowers violet, of two kinds, the cleistogamous fertile, the petaliferous sterile; including all remaining species. These generalizations are not entirely accurate. Members of the L. capitata group usually possess some cleistogamous flowers; they are the inner flowers in the dense clusters and are not easily seen. On the other hand, cleistogamous flowers are not invariably characteristic of the violet flowered species – or if present, may wither away without setting fruit; the petaliferous flowers are not necessarily sterile, although they frequently appear to set seed less abundantly than cleistogamous ones.

Among the violet-flowered lespedezas the petaliferous flowers are in raceme-like inflorescences, while the cleistogamous ones are usually axillary and sessile and possess a smaller calyx than the petal-bearing flowers; their lobes are frequently broader and shorter than those of the former. There is considerable variation in the occurrence and the seed-set by the cleistogamous flowers – in some cases, axillary pods are abundant; in others they are entirely absent. Since this phenomenon may be observed in most species, it would appear to have little taxonomic significance. The behavior of the petaliferous flowers is likewise variable; in some cases the flowers appear almost entirely sterile; in other instances they set abundant fruit. The cause of sterility does not seem to be, as has been inferred by some authors, that the flowers are staminate; numerous flowers have been examined, and a pistil was invariably present. However, such a differential fertility could result if the petaliferous flowers were self-sterile, and required the activities of pollinating insects. Schindler (1913) refers to "parthenogenischen Früchten" produced by the apetalous flowers. It is not clear whether he means this

literally (in terms of the modern definition of the term) or whether he is merely inferring that the flowers are self-fertilized. With regard to the introduced Asiatic species, L. striata and L. stipulacea, Helm (1951) comments that both the petaliferous and apetalous flowers are normally self fertilized, that both set seed, and that while the porportion of the two types varies greatly from season to season, this fact appears to have little relationship to seed production.

The American lespedezas form a relatively close knit (and presumably related) group of species whose precise intra-specific limits are sometimes difficult to define. It could easily be held that these difficulties might be the result of a poor understanding of the species, and that the characters on which they are based are of less than fundamental importance. I entertained this theory at one time but have gradually rejected it on the basis of accumulated observations. The native American Lespedeza species, as currently delimited, appear essentially sound—but they must be recognized to be species of a type which—closely related and polymorphic—may not be definable to the last specimen.

It is frequently said that the American lespedezas hybridize with one another—for instance, Fernald (1950) attributes wide scale intra-specific crossing to most species. Such an assumption is not unreasonable in light of observed intra-specific variability, but it should be borne in mind that all such Lespedeza hybrids are putative—no direct evidence of crossing between different species has been presented. It might be equally as reasonable to inquire if the American lespedezas, or at least some of them, might not yet be in an early stage of evolution (as species) and that complete isolation, one from another, of the various interbreeding populations had not yet been achieved. To the author this hypothesis is particularly suggestive in regard to the L. virginica - intermedia - stuevei complex—a group of closely related species, each containing within its range of variability a sequence of forms "slanting" towards the other species—in which a parallel series of leaf and fruit types occurs within each species. Young (1940) studying the cytology of this genus, not only found the chromosome number of all species to be the same (somatic 20) but, investigating several supposed hybrids, observed no chromosome irregularities. He commented, "If hybridization does occur in Lespedeza it is apparently attended by complete compatibility of the parental chromosomes."

Trends of intra-specific blending, and apparent identity of putative intermediates are plotted in Plate XIV. The chart does not necessarily imply that such intermediates are hybrids—they are merely placed according to their apparent morphological identity.

Cytological studies of Lespedeza have been made by Young (1940), and Pierce (1939). Other workers have reported on a few species. The majority of species have been indicated to be diploids with somatic chromosome numbers of 20 or 22. All of the American species tabulated by Young had a somatic 20. A gametic number of 9 has been reported for several species—to the extent that Senn (1938) believed it to be the basic number for the genus. Young (l.c.) however, observed that several species, exhibiting only 9 bivalents in microspore mother cells, definitely had 20 chromosomes in root tip preparations. He felt it probable, in such instances, that the tenth pair was hidden by the nucleolus.

Three introduced species of *Lespedeza* (*L. striata* and *L. stipulacea*, annuals; *L. cuneata*, perennial) are widely employed for hay, forage, and green manure crops in the southern states, and the last species has proved valuable for soil conservation purposes in the southeast. Several additional Asiatic species are undergoing testing by agricultural experiment stations and the Soil Conservation Service at the present time and are highly recommended (especially *L. bicolor*) by Davison (1948). The native species are said to be valuable for wild life maintenance by Graham (1941), but their value is questioned by Davison (l.c.). They are pioneers in the invasion and revegetation of impoverished or disturbed soil. They appear to be relished by stock (rapidly disappear in pastured areas), and presumably have forage value. However, they have received little experimental attention.

Literature

- Blake (1924), Misc. notes.
 Deam (1940, 610-615), Indiana spp.
 Fassett (1939, 98-110), Wisconsin spp.
 Fernald (1941), *L. capitata* and *hirta*.
 Fernald (1950, 923-927), eastern United States.
 Fox (1945, 224-225), Iowa spp.
 Graham (1941, 62-67), use by wild life.
 Helm (1951), cultivated spp.
 Hopkins (1935), *L. virginica* and relatives.
 Isely (1948), *L. striata* and *stipulacea*.
 Jones (1945, 167-168), Illinois spp.
 Pierce (1939), chromosome numbers.
 Pieters (1939a), *L. sericea*.
 Rydberg (1932, 490-492), central United States.
 Schindler (1912, 1912a, 1913), world-wide survey of genus.
 Young (1940), chromosome numbers.

Key to Species of Lespedeza

1. Stipules conspicuous, broad, membranous or scarious; plants annual, prostrate or low ascending. (Plate XVII, Fig. 4)
2. Stems retrorse-strigose; leaves mostly appearing subsessile, not conspicuously ciliate; calyx 1/2 - 4/5 covering fruit. (Plate XVII, Figs. 1-3) *Lespedeza striata*
2. Stems upwardly-strigose; leaves mostly with distinct petioles (4-10 mm. long on main stems); margin and lower midrib of young leaflets conspicuously ciliate; calyx 1/3 - 1/2 covering fruit. (Plate XVI, Figs. 4-6) *L. stipulacea*
1. Stipules inconspicuous, subulate; plants perennial, usually erect or ascending - two species prostrate vines. (Plate XII, Fig. 5)

3. Calyx approximating or longer than pod.
(Plate XI, Fig. 4)
 4. Flowers purplish; plants of local distribution, primarily in Missouri.
 5. Petaliferous flowers in capitate spikes; peduncles shorter than leaves; leaves frequently silvery-pubescent beneath. L. simulata
 5. Petaliferous flowers racemed, the peduncles mostly exceeding the leaves; leaflets frequently sparsely strigose beneath. L. manniana
 4. Flowers yellowish-white; plants widely distributed.
 6. Inflorescence of slender, loosely-flowered axillary spikes which strongly exceed subtending leaves; medial and upper leaflets narrowly oblong. (Plate XIII, Figs. 1-3) L. leptostachya
 6. Inflorescence of closely flowered or head-like, congested racemes which exceed or are overtopped by subtending leaves; leaflets various, usually not narrowly oblong. (Plate XII, Fig. 1)
 7. Calyces approximating legumes, usually less than 8 mm. in length; racemes usually overtopping leaves, cylindric, the flowers divergent; leaflets obovate to elliptic (rare exceptions in east). (Plate XII, Figs. 1-3) L. hirta
 7. Calyces exceeding legumes, usually more than 8 mm. in length; racemes head-like, usually shorter than subtending leaves; flowers ascending, the innermost hidden from view; leaflets typically oblong or narrowly elliptic (some exceptions). (Plate XI, Figs. 1-4). L. capitata
3. Calyx shorter than pod; flowers usually purplish. (Plate XIII, Fig. 4)
 8. Plants trailing vines. (Plate XVI, Fig. 1)
 9. Stems spreading-hirsute; racemes mostly 6-10 flowered. (Plate XV, Figs. 1,2) L. procumbens
 9. Stems appressed-puberulent; racemes mostly 4-6 flowered. (Plate XVI, Figs. 1-3) L. repens
 8. Plants erect or ascending, not vine-like.

10. Petaliferous flowers purplish, in peduncled or sessile, glomerate, 4-many flowered racemes; leaves various. (Plate XVIII, Figs. 2,5)
11. Racemes of petaliferous flowers pedunculate, at least some of them definitely exceeding leaves (note: plants may also have numerous, axillary subsessile fruits produced from apetalous flowers). (Plate XVIII, Fig. 2)
12. Racemes spike-like 8-14 flowered; calyx 4-6 mm. long, $1/2 - 3/4$ as long as pod; stems, calyces and pods finely villous. (Plate XIII, Figs. 4-6) L. nuttallii
12. Racemes 4-6 flowered; calyx (petaliferous flowers) 2-4 mm. long, about $1/2$ as long as pod; stems, calyces and pods sparsely strigose. (Plate XVIII, Figs. 1-3) L. violacea
11. Racemes of petaliferous flowers short-pedunculate or axillary-glomerate, not exceeding subtending leaves. (Plate XVIII, Fig. 5)
13. Calyces, fruits, and lower surface of leaves villous. (Plate XVII, Figs. 4,5) L. stuevei
13. Calyces, fruits and leaves sparsely strigose. (Plate XVIII, Figs. 4-6)
14. Leaflets narrowly oblong. (Plate XVIII, Figs. 4-6) L. virginica
14. Leaflets ovate or elliptic. (Plate XII, Figs. 4-5) L. intermedia
10. Petaliferous flowers yellowish-white, in axillary 2-3 flowered clusters, leaves all short-petioled; leaflets wedge-shaped, strongly apiculate. (Plate XI, Figs. 5,6) L. cuneata

Key to Species of Lespedeza - Vegetative Characters¹

1. Stipules broad, membranous or scarious; plants annual, prostrate or ascending. (Plate XVI, Fig. 4)
 2. Stems retrorse-strigose; leaves mostly appearing subsessile; leaflets obovate to narrowly elliptic, neither conspicuously ciliate nor emarginate. (Plate XVII, Fig. 1) Lespedeza striata
 2. Stems upwardly strigose, leaves mostly distinct petioled (petioles 4-10 mm. long on main stems); leaflets broader than above, spatulate to obovate, apically emarginate, when unfolding conspicuously ciliate along margins and lower midrib. (Plate XVI, Fig. 4) L. stipulacea
1. Stipules inconspicuous, subulate; plants perennial, usually erect or ascending - two species prostrate vines. (Plate XII, Fig. 5)
 3. Plants prostrate, vine-like. (Plate XVI, Fig. 1)
 4. Stem pubescence appressed; leaflets elliptic to obovate, frequently twice as long as broad. (Plate XVI, Figs. 1,3) L. repens
 4. Stem pubescence spreading, leaflets ovate, usually not twice as long as broad. (Plate XV, Figs. 1,2) L. procumbens
 3. Plants erect or ascending.
 5. Stems conspicuously ridged, with pubescence primarily in lines on these ridges; leaflets wedge-shaped and apiculate, gray-strigose when young; plants cultivated and occasionally escaped in south. (Plate XI, Fig. 5) L. cuneata
 5. Stems inconspicuously ridged or striate; pubescence not in lines; leaflets various, rarely wedge-shaped; native species. (Plate XI, Figs. 2,3)
 6. Leaves villous or sericeous beneath. (Plate XVII, Fig. 4)

¹ It is not possible to construct a simple key that will, in all cases, distinguish the following species of Lespedeza on the basis of vegetative characters. Distinctions must be prognosticated primarily upon leaflet shape and pubescence, characteristics which are variable in several species. Unless one is intimately familiar with the lespedezas, key determinations should be carefully checked against descriptions and known specimens. Also, the uncommon intermediate forms, L. manniana and L. simulata, which cannot be identified unless in flower, are not included in the key.

7. Stem pubescence appressed; lower leaves broadly oblong, upper becoming narrowly oblong to linear; stalk of terminal leaflet not exceeding 5 mm.; uncommon prairie species of northern Iowa and adjacent Minnesota. (Plate XIII, Figs. 2,3) L. leptostachya
7. Stem pubescence spreading; lower and upper leaves mostly essentially similar in shape; stalk of terminal leaflet usually exceeding 5 mm.; widely distributed species. (Plate XI, Fig. 2)
8. Principal leaflets usually 3-5 mm. long, oblong to narrowly elliptic; stipules 3-nerved. (Plate XI, Figs. 2,3) L. capitata
8. Principal leaflets usually 1-3 mm. long, broadly ovate (or, var. angustifolia primarily of Arkansas and Texas, elliptic to oblong); stipules without evident nervation. (Plate XVII, Fig. 4). L. stuevei
6. Leaves strigose or puberulent-hirsute beneath. (Plate XVIII, Fig. 4)
9. Leaflets oblong or narrowly elliptic, more than three times as long as broad. (Plate XVIII, Fig. 4)
10. Stem pubescence usually scant, appressed; main leaflets mostly 2-3 (4) cm. long; stipules not discernibly nerved. (Plate XVIII, Fig. 4) L. virginica
10. Stem pubescence usually spreading; main leaflets 3.5-6 cm. long; stipules usually discernibly 3-nerved. (Plate XI, Fig. 3) L. capitata
9. Leaflets ovate to elliptic or broadly oblong, usually not more than two and one-half times longer than broad. (Plate XII, Figs. 2,4)
11. Stems pilose or hirsute with spreading pubescence. (Plate XII, Fig. 2)
12. Younger portions of stems velvety-puberulent; leaves mostly with petioles much shorter than length of terminal leaflet; stipules striate. (Plate XII, Fig. 2)

13. Leaflets broadly elliptic or obovate, not more than one and one-half times as long as broad. (Plate XII, Fig. 2). L. hirta¹
13. Leaflets elliptic to broadly oblong. (Plate XI, Fig. 2). L. capitata
12. Stems pilose or hirsute; petioles of most leaves approximating terminal leaflet; stipules not discernibly striate. (Plate XIII, Fig. 5). . . L. nuttallii
11. Stems strigose or glabrate. (Plate XII, Fig. 4)
14. Plants closely leafy, usually little branched and "wand like". (Plate XII, Fig. 5) . . L. intermedia
14. Plant loosely leafy, usually with divergent or somewhat arching branches. (Plate XVIII, Fig. 3) L. violacea

LESPEDEZA CAPITATA Michx. (Incl. L. longifolia auth., not DC.)
(Plate XI, Figs. 1-4. Map 21)

Stems erect, usually simple below inflorescence, closely leafy. Leaves subsessile to short-petioled (0.5 cm). Leaflets usually oblong or narrowly elliptic but ranging from obovate to linear-lanceolate; thinly to densely sericeous beneath, or spreading-villous; appressed silky to glabrate above. Racemes dense, short-peduncled, spike- or head-like, arising in axils of leaves of main stem and glomerate on short branches at stem apex. Individual racemes - but not necessarily lower raceme-bearing branches - scarcely overtopping subtending leaves except at tip of stem where leaves may be reduced. Flowers ascending, overlapping, the innermost usually hidden, concealing raceme axis. Calyces hairy, usually 8-10 (12) mm long, approximating corolla. Petals yellow-white, the standard with a purple spot. Pod weakly nerved, shorter than calyx.

L. capitata ranges over the eastern United States (except for peninsular Florida) and adjacent Canada west to eastern Texas and central South Dakota. Its greatest abundance appears to be in the northern states, and it is one of the most common native legumes in the north-central area.

¹An uncommon eastern coastal plain form--with narrow leaflets--is omitted from the key.



PLATE XI. LESPEDEZA

Lespedeza capitata, 1. Inflorescence x 1. 2. Leaf, a form with broad leaflets x $2/3$. 3. Leaf, a form with narrow leaflets x $2/3$. 4. Mature fruit invested by calyx x 5. L. cuneata, 5. Leaf and stipule x 2. 6. Flower-bearing portion of stem x 2.

It occurs in a variety of habitats, usually sandy soil, dry and/or rocky, wooded hillsides, glades, roadsides, prairie remnants. Fassett (1939) states that it has invaded many areas following the destruction of the forests. Blooming is usually initiated about the first week in August and fruit is matured (approximately) 10th to 20th of September.

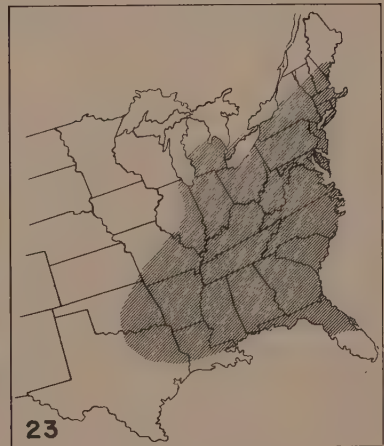
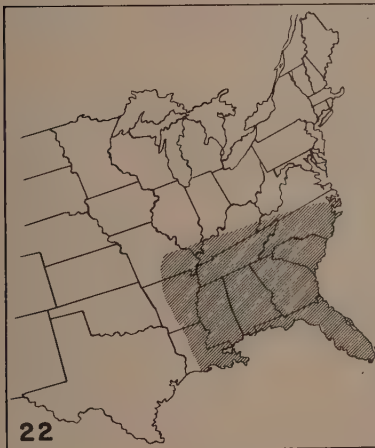
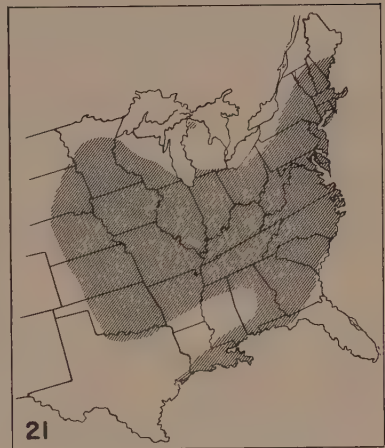
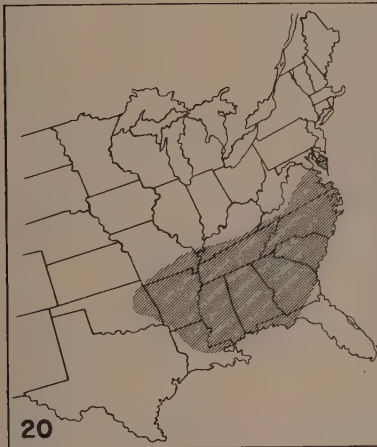
Lespedeza capitata is variable with respect to the amount and nature of leaflet pubescence, leaflet shape, and the degree to which the flower aggregates hide the subtending leaves. Authors are not in general agreement regarding the validity of varietal categories characterizing this variation. The treatment in the current Gray's manual (Fernald, 1950), recognizing five varieties, is based on a detailed study of L. capitata and hirta by Fernald (1941). Since this author's classification of L. capitata is widely accepted, it may be well to pass it in review. His varieties are summarized in key form below.

Key to the varieties of Lespedeza capitata

1. Leaflets linear-lanceolate. Var. stenophylla Bissell & Fern.
(L. longifolia, L. capitata longifolia auth., not DC.,
fide Fernald)
1. Leaflets oblong to ovate.
 2. Leaflets broadly ovate; peduncles frequently somewhat elongate, approximating or exceeding subtending leaves. Var. calycina (Schindl.) Fern.
 2. Leaflets oblong to narrowly elliptic; peduncles various, usually shorter than subtending leaves.
 3. Leaflets densely puberulent or pilose beneath with spreading or recurved hairs. Var. velutina (Bickn.) Fern.
(L. bicknellii House;
L. velutina Bickn.)
 3. Leaves appressed-sericeous beneath.
 4. Leaflets brightly sericeous on lower surface, grey-pubescent above; heads usually hiding subtending leaves. Var. capitata (var. sericea Hook. and Arn.;
var. typica of Fern.)
 4. Leaflets dull beneath, glabrate above; heads not hiding subtending leaves. Var. vulgaris
T. and G. (typical variety of
older treatments)

Of the above, varieties capitata and vulgaris constitute the bulk of the species. Variety capitata is said to predominate on the eastern and south-eastern coastal plain but is also "common southwest and west" (Fernald,¹

¹"Typical" L. capitata of Fernald's treatment. This would be variety capitata under present rules of nomenclature.



20. Desmodium viridiflorum. 21. Lespedeza capitata.
 22. L. cuneata. 23. L. hirta.

1950). Variety vulgaris is the common inland, north-central states form. It is obvious from states cited (Fernald 1941, 1950), however, that the two widely overlap. Variety calycina is a southeastern form which in leaf and inflorescence characters looks like L. hirta (under which it was originally described by Schindler). Variety stenophylla, a narrow-leaved form, apparently occurs throughout much of the range of the species. Variety velutina is said to be characteristic of the northeastern states.

Fernald's concepts of both L. capitata and L. hirta may be summarized under the following points.

(1) The species are polymorphic.

(2) The two species intergrade and populations represented by several varieties can be assigned to the proper species only with difficulty.

(3) In regard to distinguishing between the species, the length of the calyx and the dense, upwardly appressed, overlapping flowers of L. capitata are emphasized. The taxonomic value of the comparative peduncle length and leaflet shape is minimized.

(4) The varieties are relatively distinct—in fact less is said concerning intermediates between varieties than between the two species. Several of the varieties are defined in terms of combinations of pubescence of leaflet, and inflorescence characters. The author is able not only to delimit the "pronounced geographic concentration" of each, but, within local regions where several forms occur, in some cases, to give details of precise areas or soil types occupied by each (Fernald, 1941, pp. 581-582).

To some extent my observations have differed from those of Dr. Fernald. They are presented below following the outline form given above.

(1) The species are variable, but no more so than several of our native lespedezas. If one is to divide L. capitata and hirta into a series of varieties, one should probably also do so for L. virginica, stuevei, and intermedia which are markedly polymorphic.

(2) Lepedeza hirta and capitata intergrade no more and possibly less than some of the other species. In the course of field observations and in the examination of about a thousand herbarium sheets of these species, I have encountered very few specimens which were difficult to place with one or the other of the two taxa. The occurrence of a few such forms does not vitiate the fact that the great bulk of the constituent populations can be defined on the basis of several contrasting characters.

(3) Calyx size and juxtaposition of the flowers, as believed by Fernald, are possibly the most important specific characteristics. However, he overemphasizes differential calyx sizes in some diagnoses. The calyces of both species are quite variable in length—as this author (i.e., Fernald, l.c. p. 573) correctly points out in his key—but the calyx of L. capitata is usually about 10 mm long, and ordinarily does not "greatly exceed the legume" but ranges from subequal to perhaps 2 mm longer. Also, in most cases, comparative peduncle length and leaflet width are diagnostic except for uncommon southeastern, narrow leaved varieties of L. hirta.

(4) I am unable to determine any cleavage of L. capitata into satisfactory geographical varieties. The species is variable with respect to several characters (enumerated above) which are variously combined in a wide range of phenotypes. Some phenotypes appear more predominant in certain parts of the country and within local areas. Some populations may be represented by a single phenotype almost to the exclusion of others. In other areas, the population may be highly heterogeneous. Fernald's varietal characterizations represent, in some cases, extremes of variability; in other instances include certain combinations of phenotypic characters but exclude others which should be equally deserving of varietal recognition.

To be specific, variety capitata (Fernald's typical variety) is said to have "leaves brilliantly silvery beneath and grayish to silvery and lustrous above and with the densely crowded upper spikes mostly overtopping their subtending leaves," while var. vulgaris is "the common northern and inland plant ... with round-tipped or obtuse oblong leaflets appressed-pubescent beneath with opaque or only slightly lustrous hairs, and green above, the capitate spikes often overtopped by their subtending leaves..." Of the above characters, so far as I can determine, there is an almost complete series from plants with leaflets sparsely strigose beneath and glabrate above (thus appearing green) to those which are very densely appressed-silvery both above and below. There is little tendency towards grouping into two categories. Although it is true that plants which are densely pubescent on the under surface of leaflets tend to be pubescent (and grayish) above, even this by no means invariably follows. Some are scantily strigose or lightly silvery both above and below, others are densely sericeous below and greenish-glabrate above; furthermore, the younger leaflets towards the apex of the stem, or the entire plant prior to flowering, may be quite silvery, while the older leaflets become glabrate-greenish. The degree to which the flowering spikes hide the subtending leaves may or may not correlate with the leaflet pubescence characters as specified for these varieties; i.e., silvery pubescent plants may have leafy inflorescences or vice versa; the same is true of the less hairy forms. I think it is true that the pubescent forms are more abundant in the southern part of the range of the species, but these also occur abundantly in the "northern and inland" areas; for instance, are amply represented among Iowa and Minnesota specimens.

It is difficult to determine what forms var. velutina is intended to represent. By description it is indicated to be "densely velvety-pilose, with dull to sublustrous to fulvous pubescence ... northeastern." One would expect densely hairy plants, but those specimens which I have seen carrying Gray herbarium identifications are sparsely hirsute. In general, leaflet pubescence in Lespedeza capitata is more-or-less appressed, but occasional specimens, sparsely or densely pubescent, may exhibit a somewhat spreading indument, particularly old or weathered plants.

My experience with the rare, southern variety calycina is too limited to allow comment. Various sheets which I have seen of the narrow leaved extreme, var. stenophylla, are possibly more readily identifiable than the categories discussed above.

It might be well to interpolate that other authors have expressed viewpoints somewhat similar to the above. Schindler (1913) did not include a single variety under Lespedeza capitata. Fassett (1939) reported: (1) that varietal names describe only a small proportion of the total variation of the species, (2) that, in Wisconsin, a single colony may consist of several forms of the species, (3) that, offspring may or may not resemble the parent. He took the position that none of these phenotypes merited recognition as separate species or varieties.

Young (1940) and Pierce (1939) have both reported a somatic chromosome number of 20 for this species.

LESPEDEZA CUNEATA (Dumont) Don. Sericea lespedeza (L. sericea (Thunb.) Miq.) (Plate XI, Figs. 5, 6. Map 22)

Plants perennial from a woody crown. Stems clustered, erect, closely appressed-pubescent in lines, bushy with ascending branches on upper half, closely leafy. Leaves short-petioled. Leaflets small, oblong-cuneate, broadest and apiculate at apex, appressed-pubescent. Flowers in 2-3 (4) flowered clusters on short peduncles on main stem and branches, whitish. Calyx about 2.5 mm long. Pod scarcely nerved, puberulent, slightly exceeding calyx. Seeds ovate, slightly notched, yellowish, brownish-speckled.

Sericea lespedeza is native in eastern temperate Asia. It is widely cultivated and escaped in the southeastern United States. In the north-central states area it occurs only in southern Missouri, its usefulness and ability to establish itself as an escape further north being limited by lack of winter hardiness and inability to set seed.

It is unfortunately necessary to follow recent authors who have taken up Lespedeza cuneata (Dumont) Don in place of L. sericea (Thunb.) Miq. The latter binomial is based on Hedysarum sericeum Thunb. Fl. Jap. 287 (typ. 289), 1784 which is antedated by H. sericeum Mill. Gard Dict. (pages not numbered), 1768—hence a later homonym.

L. cuneata blooms in late summer and matures fruit in September or early October.

Cooper (1936) reports a somatic chromosome number of 18 for sericea lespedeza; this is verified by Pierce's (1939) gametic 9.

First tested by the U.S.D.A. about 1900, but given little attention until 1925, this plant now finds favor for soil improvement, wildlife, forage, and to a lesser extent for hay. It will thrive on marginal or acid soils where other legumes fail, but is not as desirable as the annual lespedezas for forage or hay. However, where soil erosion control or soil improvement is the major consideration, sericea lespedeza is probably the most valuable plant available. Its ability to produce a dense stand on unproductive soils or steep gullies, to withstand summer drought, to form litter, to compete successfully with other vegetation, and its value as cover and food to wildlife all contribute to its usefulness.



PLATE XII. *LESPЕДЕЗА*

Lespedeza hirta, 1, Inflorescence $\times 1-1\frac{1}{3}$. 2. Leaf and stipules $\times 1-1\frac{1}{3}$.
 3. Mature fruit with investing calyx $\times 4$. *L. intermedia*, 4. Leaf and
 stipule $\times 1$. 5. Fruit-bearing portion of stem $\times 2\frac{2}{3}$.

LESPEDEZA HIRTA (L.) Horn. (Plate XII, Figs. 1-3. Map 23)

Stems erect, puberulent or pilose, simple or branched above. Leaflets broadly obovate to elliptic, rarely narrowly oblong or linear, pubescent beneath. Inflorescences of cylindrical, axillary racemes on peduncles which usually exceed the subtending leaves; on small plants the racemes arise directly from the unbranched main stem; on larger ones, except at apex of main axis, they arise from leafy branches on upper portion of stem. Flowers mostly divergent, aggregated at tips of peduncles, not completely hiding raceme axis; fruits becoming appressed and frequently covering axis. Calyx hairy, 5-8 (10) mm long, usually longer in fruit than flower. Petals yellow-white, the standard with a purple spot. Pod approximating or slightly shorter than calyx, villous.

This species may be found throughout most of the eastern United States from New England to Michigan, southwest to eastern Texas, east to Florida. It occurs primarily in the eastern half of the north-central region - extending to southern Missouri - usually in dry, open, upland woods, almost entirely in acid soils. In Indiana, Deam (1940) states that it is to be found in acid, sandy, or gravelly soils on the crests of black oak or black and white oak wooded ridges. In the southeastern part of its range the plant is frequent in pine scrub or oak-pine woodland.

In the northern portion of its range, *L. hirta* comes into bloom the first to middle part of August. In the southern states, blooming may not be initiated until September, and plants still in flower may be found in October. Seed is apparently matured about a month after flowering.

Varieties of *L. hirta*, characterized in detail by Fernald (1941) are summarized below.

Key to the varieties of *Lespedeza hirta*

1. Leaflets obovate or broadly elliptic, 1.5-2.5 times as long as broad.
 2. Stems and leaves with spreading, pilose pubescence. Var. *hirta*
 2. Stems densely puberulent; leaflets silvery appressed-puberulent, small. Var. *appressipilis* Blake.
1. Leaflets oblong to linear, 3-8 times as long as broad.
 3. Peduncles shorter than subtending leaves. Var. *dissimulans* Fern.
 3. Peduncles exceeding subtending leaves.

4. Leaflets oblong, 3-5 times as long as broad;
calyx 6-8 mm. in length. Var. longifolia (DC.) Fern.
(not L. longifolia auth.)
4. Leaflets linear, 5-8 times as long as broad;
calyx 8-10 mm. in length. Var. intercurva Fern.

Of the above, other than the widespread typical variety, variety dis-simulans is the only one which Fernald (l.c.) reports from the north-central states (Wisconsin). His characterization is this variety indicates it to be intermediate between L. hirta and L. capitata, having the inflorescence characters of the latter and the calyx and pods of the former. Of the other named variants, the narrow-leaved longifolia and intercurva have been interpreted as possibly representing intermediates between L. hirta and the coastal plain L. angustifolia.¹ Variety appressipilis characterized by its pubescence and small leaves is said to be restricted to the southeastern coastal plain.

Nearly all of the material, seen by the present author in the herbarium and field, has been of the typical species. Narrower-leaved forms are of occasional occurrence in the north-central states and presumably might be assigned to variety longifolia, although, according to Fernald (l.c.), this would be outside of the range of that form. Also, there appears to be a predominance of small-leaved forms in the southeastern United States. Some of these are densely velutinous with fine pubescence and could be referred to Blake's appressipilis.

An unfortunate aspect of a tabulation of numerous varieties, as given above, is that it may result in an erroneous impression of the variability of the complex. On the whole, Lespedeza hirta is a consistent and easily recognized species; the variants are sporadic in occurrence or limited in range (primarily eastern coastal plain).

Interrelationships between L. hirta and L. capitata are treated in detail under the latter.

Young (1940) and Pierce (1939) report a somatic 20 chromosomes for L. hirta.

LESPEDEZA INTERMEDIA (Wats.) Britt. (Lespedeza frutescens authors, not Hedysarum frutescens L.) (Plate XII, Figs. 4, 5. Map 24)
Stems ascending, appressed-puberulent or infrequently pilose, usually closely leafy. Leaflets ovate to oblong. Racemes in upper leaf axils or on short branches, short pedunculate, glomerate at apex of stem. Petaliferous calyces 3-5 mm long. Petals violet. Pods 5-7 mm long, sparsely strigose.

L. intermedia occurs throughout most of the eastern United States west to eastern Texas and Kansas. It is found in the north-central states south of a line extending southwest from southern Michigan to eastern Texas. The plant is common, particularly in the southern and eastern portion of

¹ Considered by Schindler (1913) as a variety of L. hirta.

its range, in sterile woodlands and open areas, primarily in slightly acid soil. In the northern part of its range it flowers about the middle of August; in the southern states, however, blooming is usually delayed until September.

The nomenclature of this species, with respect to the application of the name L. frutescens (L.) Horn, -not (L.) Britt. as usually cited-is discussed in full by Blake (1924).

Vegetatively, L. intermedia is variable as to pubescence, width of leaflets, size and degree of crowding of leaves on the mainstem. Loosely leafy plants with large, thin, long-petioled blades appear difficult to associate with typical L. intermedia, but are indistinguishable in flower and fruit. Specimens with unusually narrow leaflets are perhaps only arbitrarily distinguishable from L. virginica, on which basis Schindler (1913) considers L. intermedia as a variety of L. virginica; such forms are, however, relatively uncommon.

As to pubescence, the common ("typical") form of L. intermedia is scantily or moderately strigose. Such plants are not sharply distinguishable from more abundantly hairy plants with spreading pubescence (forma hahnii (Blake) Hopkins), which in their extreme form are much confused with L. stuevei. The distinctions are discussed under the latter species.

Young (1940) obtained somatic and gametic chromosome determinations of 20 and 9, respectively, for this species (as L. frutescens). He believed the somatic figure to be the correct one.

LESPEDEZA LEPTOSTACHYA Engelm. (Plate XIII, Figs. 1-3. Map 25)
Stems erect, appressed-hairy. Leaflets appressed-sericeous, those on lower part of stem obovate to oblong, the upper narrowly oblong and subsessile. Racemes spike-like, when fully elongated much exceeding leaves, loosely flowered. Calyx teeth lance-subulate. Petals yellowish. Pod 4-5 mm long, villous, slightly shorter than calyx. Seed yellowish; hilum lateral.

L. leptostachya is an uncommon prairie species, originally native to a limited area in southern Minnesota and Wisconsin and northern Iowa and Illinois. Fassett (1939) states that it is now apparently extinct in Wisconsin, and it has probably suffered a similar fate at many stations in the neighboring states.

The plant flowers in August and matures fruit in late August or September.

LESPEDEZA MANNIANA Mack. and Bush

Stems and leaves appressed- or spreading-puberulent. Leaflets broadly elliptic to oblong. Racemes exerted, or some of them included. Petals purple. Calyces of petaliferous flowers 6-8 mm long, approximating pod. Axillary, apetalous flowers with reduced calyces sometimes present.

Plants of the L. manniana type appear most frequently in Missouri, but are occasionally encountered elsewhere in the eastern United States.

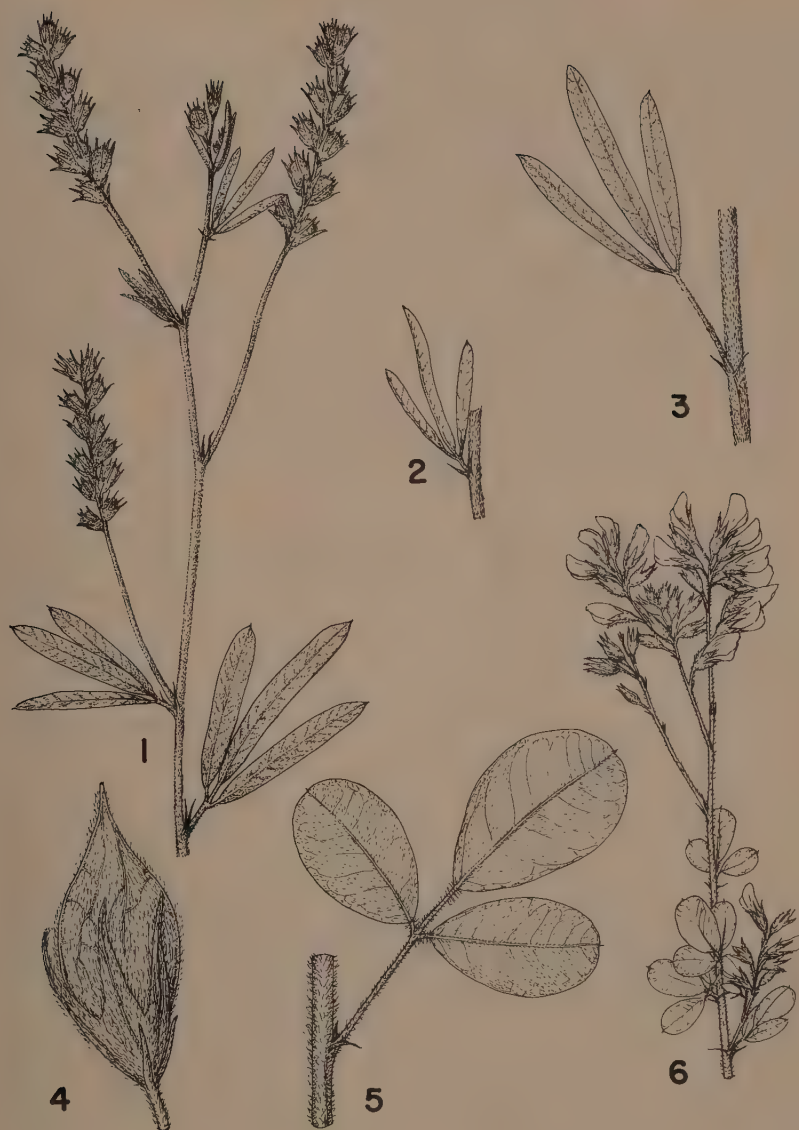


PLATE XIII. LESPEDeza

Lespedeza leptostachya, 1. Inflorescence $\times 1\frac{1}{3}$. 2. Leaf from upper portion of stem with short petiole $\times 1\frac{1}{3}$. 3. Leaf from lower portion of stem with long petiole $\times 1\frac{1}{3}$. *L. nuttallii*, 4. Mature fruit with investing calyx $\times 5$. 5. Leaf and stipule $\times 1$. 6. Portion of inflorescence $\times 1$.

They combine the calyx characters of L. hirta or L. capitata with the corolla color of the violet-flowered group, and like L. simulata are possibly of hybrid origin. Specifically, most L. manniana might appear to represent the result of crosses between L. hirta and any of several violet-flowered species—L. nuttallii, L. virginica, L. stuevei, or L. intermedia; in the same vein, L. simulata would represent similar crosses, but with L. capitata as the putative yellow-flowered parent.

LESPEDEZA NUTTALLII Darl. (Plate XIII, Figs. 4-6. Map 26)

Stems erect, simple or branched above, usually villous. Stipules subulate, 5-6 mm long, persistent. Leaflets elliptic, pubescent beneath. Racemes 8-14 flowered, distinctly peduncled, the lower in axils of leaves, the upper frequently congested. Calyx 4-6 mm long; strigose or pilose. Petals violet. Pods somewhat hairy, 6-8 mm long, enveloped for $1\frac{1}{2}$ - $3\frac{1}{4}$ of their length by petaliferous calyces. Apetalous fruits abundant or absent.

L. nuttallii occurs primarily in the south-central and eastern states, west to eastern Kansas, southeast to Florida. Its distribution in the north-central states is sporadic; e.g., it is present in southern Michigan, but appears absent from northern Indiana and Illinois; it is recorded from southern Iowa, but not northern Missouri. Hence, the appended distributional map presents a somewhat over-simplified picture of the occurrence of this species. L. nuttallii is encountered in dry woods and open areas; flowering in August or September in the northern states, sometimes as early as July in the southern portion of its range.

In its typical form, L. nuttallii is rather easily recognized, characterized by its villous stems, spike-like inflorescences, large calyces and pubescent loment. In the southeastern states, it appears to be replaced by, or merges with, forms with finely puberulent or strigose stems, smaller calyces and more congested racemes. The species is quite variable as to degree of exsertion of the racemes, and distinctions between it and hairy extremes of L. intermedia are, at times, problematic. The length of the calyx relative to the pod is likewise subject to variation and it is difficult to find a definite demarcation between L. nuttallii and some forms of the so-called L. manniana.

Young (1940) has reported a gametic chromosome number of 10 for three different collections of L. nuttallii. He indicated that two of his specimens possessed certain characters of other species, and that pollen grain size was variable; however, no chromosomal irregularities were observed.

LESPEDEZA PROCUMBENS Michx. (Plate XV, Figs. 1,2. Map 25)

Stems trailing, forming prostrate mats, closely hirsute. Leaflets ovate to elliptic, finely hirsute. Racemes axillary, 6-10 flowered at apex, exceeding leaves. Calyces 1.5-3 mm long. Petals violet. Pods mostly 4-6 mm long, nearly twice as long as petaliferous calyx.

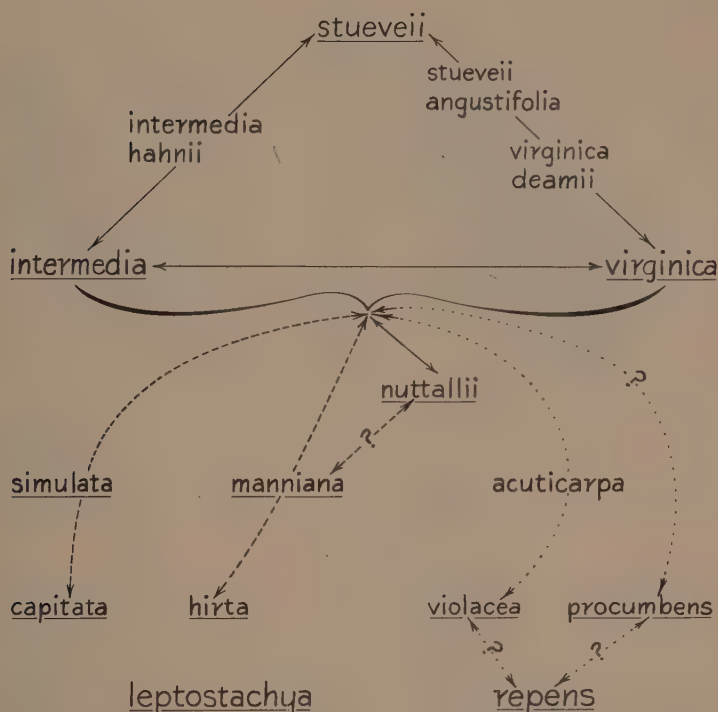
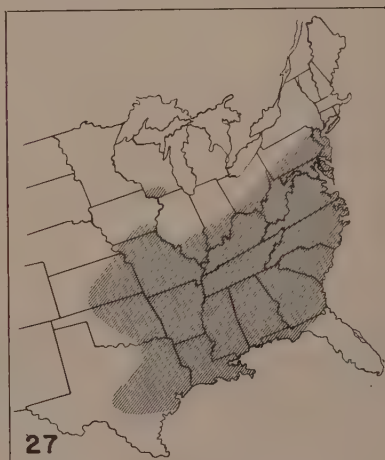
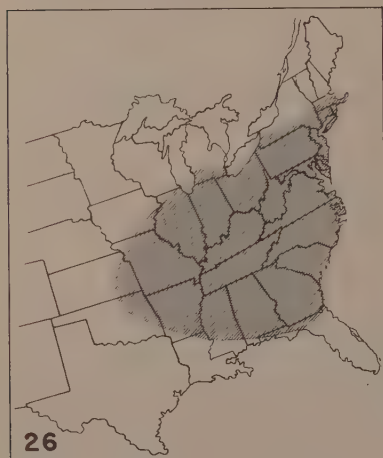
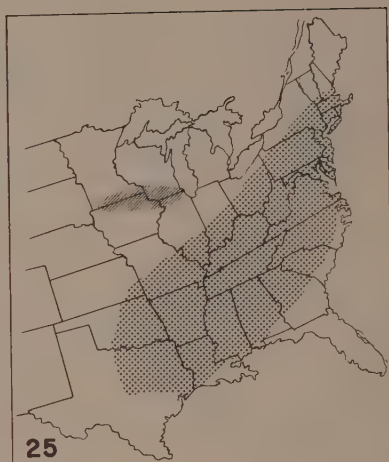
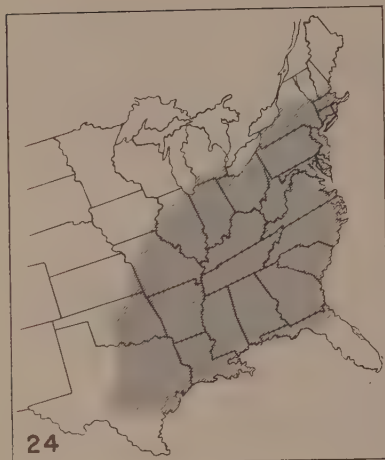


PLATE XIV. SPECIES OF *LESPEDEZA* AND INTERMEDIATE FORMS. The connecting lines indicate the presence of intermediate forms between species; greater frequency of such forms is suggested by the solid lines in comparison to the broken or dotted lines. The putative relationship of named varieties and intermediate "species" is also indicated. The arrows terminating at the brackets signify intermediates between the subject species and any member of the virginica-intermedia-steuvei triangle.

This species is common primarily along a northeast line from south-central Texas to New England. In the north-central states it may be found in southern Missouri, Illinois and Indiana. Gates reports it from Chautauqua Co. (southern border) Kansas. A single specimen (collected in 1861) records the occurrence of the species in southern Wisconsin. Fassett (1939), however, has visited the locality concerned and failed to locate the plant. Presumably the colony has been destroyed. I have seen a specimen from Cass County, Michigan, a collection which likewise seems to stand apart from the principal distributional area of the species. In the southern part of its range, L. procumbens is exceedingly common



24. Lespedeza intermedia. 25 L. leptostachya, hatched; L. procumbens stippled. 26. L. nuttallii. 27. L. repens.

in dry or rocky, open woods along roadsides and in waste areas, neutral to acid soils. Deam (1940), as for most species of *Lespedeza*, associates it with oak woodland. The plant usually blooms from late August to early September.

Leaflets, in the typical form of the species are rarely more than twice as long as wide. Blake (1924) has described as var. *elliptica*, forms with leaflets about four times as long as wide, citing specimens from Alabama and Virginia.



PLATE XV, LESPEDeza

Lespedeza procumbens, 1. Enlargement of stem to show spreading pubescence x 7. 2. Portion of stem to show leaves, flowers and fruits x 1-1/3.

Fernald (1950) feels that L. procumbens might best be treated as a variety of L. repens, a suggestion not without precedent since some earlier authors combined the two species. The two plants are similar as to habit, but differ as to leaf shape, nature of pubescence, form of the racemes, and comparative size of the petals. These are possibly not major distinctions, but are as fundamental as those distinguishing the majority of North American lespedezas. I would be inclined to suggest that L. procumbens is a prostrate form related to L. nuttallii (which it closely resembles in leaflet, pubescence; and inflorescence characters) while the affinities of L. repens lie with L. violacea.

Young (1940) and Pierce (1939) both found a somatic 20 chromosomes for this species. Young also determined a gametic 9 but felt that one bivalent had been missed.

LESPEDEZA REPENS (L.) Bart. (Incl. L. texana Britt.) (Plate XVI, Figs. 1-3. Map 27)

Stems trailing, appressed-puberulent. Stipules usually 2-5 mm long. Leaflets elliptic to obovate; finely puberulent. Peduncles axillary, filiform, exceeding leaves, loosely 4-6 flowered at apex. Petals violet, of about the same length (6-80 mm), or keel slightly the longest. Pod ovate, 3-4 mm long, about twice as long as petaliferous calyx.

L. repens occurs throughout the south-central and eastern United States exclusive of tropical Florida, north to southern New England, west to Texas and eastern Kansas. In the north-central states, it does not appear to be present in the Dakotas, Nebraska, Minnesota, or Michigan¹; it occurs only in southeastern Iowa, and has been found only in one location in southwestern Wisconsin to which Fassett (1939) suggests it may have been introduced. Like most other American members of this genus, it is ordinarily associated with sandy or stony, frequently acid soil in glades or clearings. In Indiana, Deam (1940) indicates it to be characteristic of chestnut oak and post oak ridges. In the northern portion of its range, this plant ordinarily blooms during the month of August or early September; in the south, however, it may be found in flower any time after the end of May.

In the field, L. repens is easily recognized by its habit and scant, strigose pubescence—the latter character distinguishing it from L. procumbens. L. texana Britt. of various manuals is said to possess larger pods than L. repens. Such plants appear to be L. repens in which most of the pods have developed from petaliferous flowers, and are somewhat larger than those produced by the apetalous ones.

Herbarium specimens, particularly if consisting of only a small portion of the plant so that the habit can scarcely be determined, may be difficult to distinguish from L. violacea. These species are indicated by various authors to differ as to leaf size, petiole length, length of pubescence trichomes, and comparative length of petals. None of these

¹Reported for Minnesota by Rydberg (1932); and from Michigan by Hauser (1947) on basis of literature reports but no voucher specimens cited.

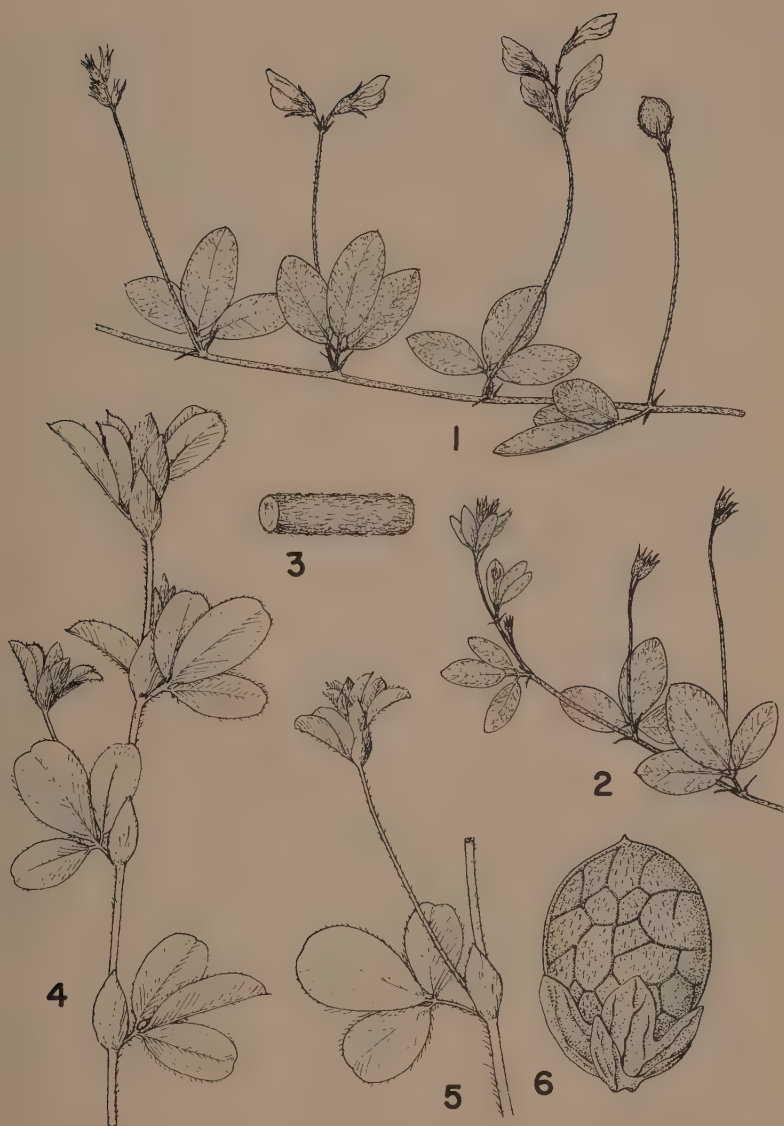


PLATE XVI. LESPEDEZA

Lespedeza repens, 1, 2. Medial and apical portions of stem respectively to show habit, flowers, and fruit x $1\frac{1}{3}$. 3. Enlarged portion of stem to show appressed pubescence x 7. L. stipulacea, 4. Apical portion of stem showing leaves and stipules x $1\frac{1}{3}$. 5. Lower portion of stem to show longer petioled leaves x $1\frac{1}{3}$. 6. Mature fruit with basally investing bracts and calyx x 10.

characters are completely dependable. Most frequently L. repens has short petioled (0.5-1.5 cm), small leaves on main stems (leaflets 1-2 cm long), and sessile blades on flowering axes. Typically, L. violacea has longer petioled (2-4 cm) blades on main stems with leaflets 2-4 cm long. However, the latter species not infrequently stimulates appearance of L. repens (whether through agency of genetic intermixing or ecological factors or both), and conversely L. repens sometimes has large, long petioled blades on the main stem. Flower size is variable for both species; the size relationship of the keel to the other petals appears less variable than other characters, but determinations are sometimes difficult to make from dried material. Fruit size and shape are not consistent in either species; the variability appears random having little relation to the identity of the specimen, or whether produced by apetalous or petaliferous flowers.

Young (1940) and Pierce (1939) both report a somatic chromosome number of 20 for this species.

LESPEDEZA SIMULATA Mack. and Bush

Stems and leaves moderately hairy to villous or silvery pubescent. Leaflets elliptic to narrowly oblong. Flower clusters spike-like, short pedunculate, and usually exceeded by leaves, frequently glomerate towards apex of stem. Corolla purple. Calyx 6-8 mm long, subequal to or exceeding pod.

L. simulata is most common in Missouri, but is probably sporadic throughout the eastern United States. I have seen collections (besides several from Missouri) from Tennessee, Pennsylvania, and New Jersey.

This anomalous species has, in varying degrees, the calyx and inflorescence characters of L. capitata, but violet flowers. The most distinctive forms, apparently localized in Missouri, appear vegetatively like silvery-pubescent L. virginica or possibly L. stuevei var. angustifolia. Other collections more closely approximate the leaf characters of L. intermedia. With respect to the presumed hybrid origin of L. simulata, it is of interest to note that Young (1940) made cytological determinations upon material said to be L. simulata, found 20 somatic chromosomes (the usual number for the genus), and stated that no irregularities were observed.

LESPEDEZA STUEVEI Nutt. (Incl. L. neglecta (Britt.) Mack. and Bush) (Plate XVII, Figs. 4, 5. Map 29)

Stems erect, usually simple below inflorescence, villous, closely leafy. Leaves mostly short petioled, typically broadly ovate (1.5-2 times as long as broad) but blending into narrowly elliptic forms. Leaflets villous, usually both above and below. Inflorescence congested; racemes all short. Petaliferous flowers violet. Calyx 3-5 mm long, hairy. Pods 5-7 mm long, short-villous.

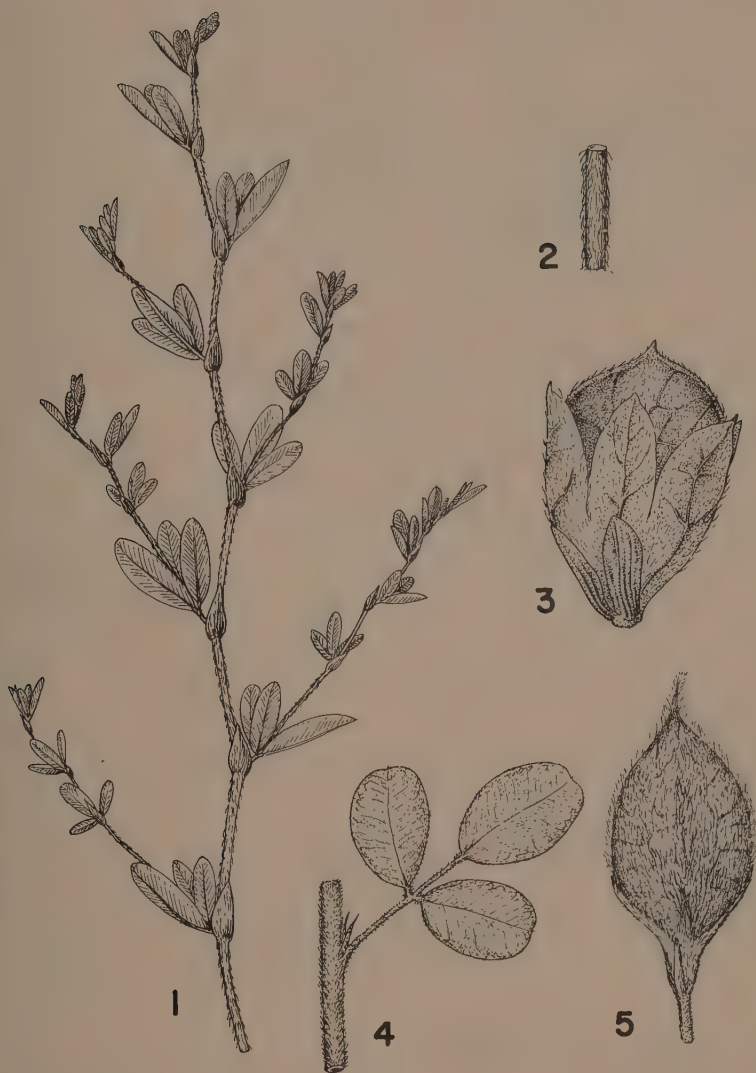


PLATE XVII. LESPEDeza

Lespedeza striata, 1. Portion of stem to show leaves and stipules $\times 1\frac{1}{3}$. 2. Stem segment with retrorse pubescence $\times 2\frac{2}{3}$. 3. Mature fruit invested by calyx and bracts $\times 10$. L. stuevei, 4. Leaf and stipule $\times 1\frac{1}{3}$. 5. Mature pod $\times 5$.

L. stuevei occupies a range similar to that of several of the native *lespedeas*, northeast to New England, southwest through the southern extremities of Indiana and Illinois to eastern Kansas and Texas, southeast to northern Florida.¹ It is locally abundant in open areas, along roadsides, and sterile woodland. Deam (1940) states that in southwestern Indiana it is found in "very sandy soil." The plant flowers in late summer.

L. stuevei is most common and easily recognized in the Ozark region of Missouri and Arkansas. Here, the predominant phenotypes are abundantly villous and possess considerably broader leaves than any other related species. To the east, it blends (or is confused) with L. intermedia forma hahnii to the extent that only somewhat arbitrary distinctions appear possible. I have considered as L. stuevei only those plants which are hairy (at least initially) on both leaf surfaces, and which possess villous pods. Much material which I have identified as a hairy form of L. intermedia has previously been called L. stuevei. I am inclined to suspect that the hairier extremes which, in the east, have been attributed to L. stuevei are more closely related to L. intermedia, and that L. stuevei proper is a midwestern and south-central unit.

Within and to the south and west of the Ozark region (and sporadically elsewhere) a narrow-leaved variant of L. stuevei is encountered. In its more pubescent phases, this plant would appear to be a leaf form of L. stuevei, but less pubescent specimens could as logically be considered hairy extremes of L. virginica. Very likely genetic material from both species is involved. These intermediate forms have been called L. stuevei var. angustifolia Britt. or L. neglecta (Britt.) Mack. and Bush.

Pierce (1939) reports a somatic chromosome number of 20 for this species, and Young (1940) a gametic 10. Young states that some of his specimens, referred to L. stuevei, were intermediate between it and L. nuttallii and that pollen grain size was variable. However, no chromosomal irregularities were observed.

LESPEDEZA STIPULACEA Maxim. Korean *lespedeza*. (Plate XVI, Figs. 4-6. Map 28)

Plants annual, reclining and much branched, or, in dense stands, erect. Stems with upwardly appressed pubescence. Stipules membranous, 5-8 mm long and 3-4 mm wide on main stems, very conspicuous at stem tips. Leaflets usually obovate, retuse at apex, about 1.4 times longer than wide; young leaflets obovate, ciliate along margins and lower midrib. Flower-bearing shoots arising from upper leaf nodes. Petals lavender.

¹Florida by report only. I have seen no specimens south of Crenshaw Co., Alabama. Hauser (1947) reports L. stuevei from Michigan. Through kindness of the herbarium curator, I have had opportunity to examine the voucher specimen which proves to be L. nuttallii. However, I have seen a Michigan specimen (Chicago Museum, Millsbaugh 3888) which appears to be somewhat intermediate between L. nuttallii and L. stuevei. Probably more information is needed in regard to the northern limits of the range of L. stuevei, or its possible genetic influence beyond this range.

Fruit rounded at apex, apiculate, distinctly reticulate with black ridges, $1/3-1/2$ covered by calyx. Seed scarcely lobed, purple-black when mature.

L. stipulacea is native to temperate eastern Asia. On the North American continent, it is established from central Iowa east to Pennsylvania, south to Georgia and Louisiana. It has occasionally been reported further to the north, but can scarcely be said to be persistent. In addition to its occurrence in cultivation, it is naturalized on and about agricultural land, around houses, along roadsides, paths, etc.

In Iowa, Korean lespedeza flowers in late August or September. In the south it may bloom considerably earlier in the summer.

Cooper (1936) reports a somatic ($2n$) chromosome number of 20 for L. stipulacea.

Korean lespedeza was introduced into the United States in 1919 for trial as an agricultural plant. Hence, it is a much more recent introduction than common lespedeza, and its spread, both in agricultural usage and as a naturalized component of the flora, has been extremely rapid. Because of this reason, it is not included in several currently employed botanical manuals, as a result of which plant specimens are frequently identified as L. striata.

The agronomic importance of the annual lespedezas is discussed in detail under common lespedeza. The area of the country in which Korean lespedeza is valuable for pasturage, hay, and cover crops is similar to that indicated for common lespedeza, except that Korean lespedeza is the more important of the two in the northern areas; it is almost completely replaced by common lespedeza in the southernmost portion of the United States.

Harbin lespedeza is a strain of Korean lespedeza, introduced from Harbin, Manchuria. It is a low-growing, small plant which is said to be capable of maturing seed as far north as the Canadian border. However, it has never become commercially important.

Several improved strains or varieties have recently been developed by plant breeders from parent stock in the United States. These differ physiologically from the unselected stock but can scarcely be differentiated on morphological grounds. Of these, Climax is a late-maturing Korean which extends the usefulness of this species further south. On the other hand, an early Korean, so-called "19604," matures seed earlier than the parent strains. Iowa 6, 39, and 48 are strains developed to meet specific needs in the state of Iowa.

LESPEDEZA STRIATA (Thunb.) H. and A. Common lespedeza (Plate XVII, Figs. 1-3. Map 28)

Plants annual. Stems much branched, prostrate or low-ascending, retrorse-strigose. Stipules conspicuous, ovate-lanceolate, usually 3-5 mm long, 1-2 mm wide. Leaves subsessile to short-petioled; leaflets obovate to narrowly elliptic. Flowers axillary, lavender to pink. Loment short-beaked, $1/2-4/5$ covered by persistent calyx. Seed black, mottled with light spots.

Common lespedeza, a native of eastern Asia, occurs throughout the south-central and eastern United States, north to central Missouri, southern Illinois and Indiana, west into eastern Kansas and Texas. Occasional collections may be recorded outside of this area, but the plant does not persist inasmuch as the northern season is too short for seed maturation, and moisture requirements limit western extension. In the southern states it is very abundant, not only in cultivation but naturalized along roadsides and paths, in abandoned fields, pastures, and open woodland, frequently persisting in dry, sterile soil where most other species fail.

L. striata and L. stipulacea are superficially quite unlike other lespedezas, being easily distinguished by their low annual habit and broad membranous stipules. On the basis of these and certain other characters (nature of branching, formation of fruit) Schindler (1912) felt that the two species should be segregated into a separate genus—Kummerowia Schindl., but considered as a single species, Kummerowia striata (Thunb.) Schindl. There is some logic in this author's generic distinction (although most subsequent writers have felt the similarities between the annual and perennial species of Lepedeza to be greater than the differences), but his decision to merge the species is completely untenable. Some of the numerous differences between common and Korean lespedeza have been tabulated by Isely (1948).

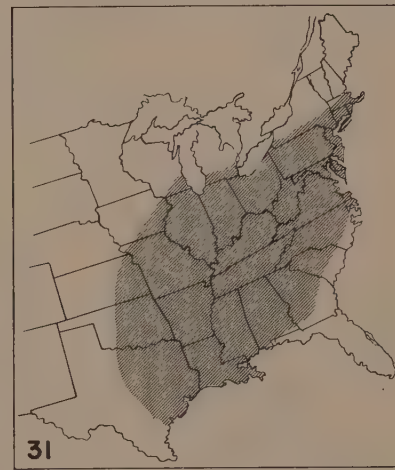
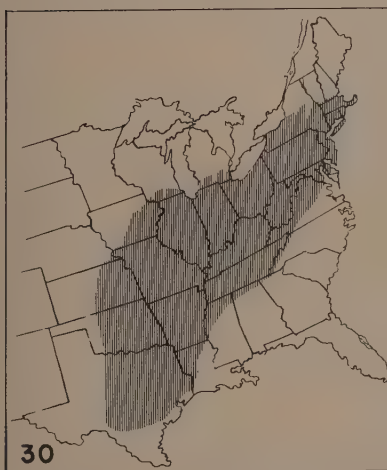
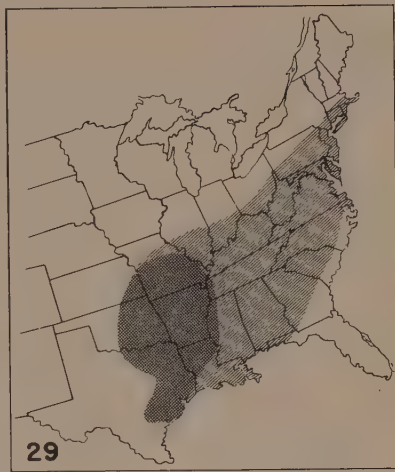
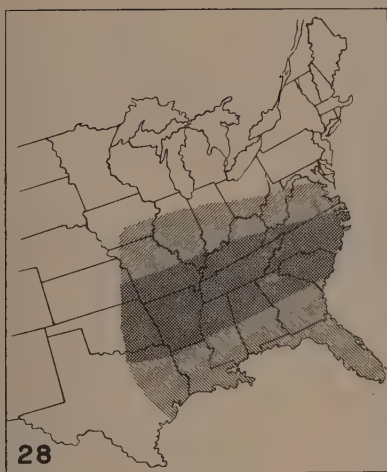
L. striata requires relatively high temperatures for seed germination and early growth in the spring. It thrives during the hot portion of the summer and blooms in late summer or early fall. The flowers are self-fertilized, and set abundant seed if the growing season is long enough. The seeds are mostly hard (impervious to water) at maturity, but, in large part, are capable of germination by the following spring particularly if they over-winter in the soil.

Pierce (1939) and Young (1940) both report a somatic 22 chromosomes for L. striata. Young comments that the chromosomes are considerably smaller than those of other species.

Common lespedeza was introduced into the Americas during the first half of the 19th century—exact date unknown. It was well established in the southeastern portion of the country by 1870 and was known as Japanese or Japan clover (and is still so designated by some botanical manuals). As its spread throughout the southern states continued, its agricultural value became evident. Seed production on a commercial basis was initiated in the early 1900's.

The annual lespedezas, common, Korean, and varieties are extensively planted for pasturage, for hay, soil improvement and as erosion control cover crops. They are especially valuable on acid soils of low fertility which would otherwise have limited agricultural utility. McKee (1948) states that lespedezas "have revolutionized agriculture over some 20 million acres of lime-deficient, sandy land in the southern and eastern parts of the United States."

Common lespedeza is particularly valuable in the southern half of the lespedeza belt because of its ability to produce forage in the late summer and fall, after Korean lespedeza has come into bloom and all but ceased growth. On the other hand, Korean is better adapted to the northern portion, starting more rapidly in the early summer months and maturing seed earlier in the fall.



28. *Lespedeza stipulacea*, northern, hatching upwardly directed to right; *L. striata*, southern, hatching upwardly directed to left. The two species overlap in the cross-hatched area. Both plants occur sporadically outside of the range indicated. 29. *L. stuevei*. Cross-hatched area indicates principal limits of var. *angustifolia*. 30. *L. violacea*. 31. *L. virginica*.

Well-known agronomic varieties of common lespedeza include, in addition to the common strains, Kobe lespedeza and Tennessee 76. Kobe lespedeza is derived from an introduction from Kobe, Japan in 1920. The plants average larger than the common form of the species and have larger, gray-pubescent calyces and larger seed. The variety is a higher yielding hay producer than common, but frequently does not reseed itself

satisfactorily, particularly if grazed late in the season. Tennessee 76 has been selected from naturalized strains of common lespedeza and is not morphologically different from them. Its usefulness is similar to that of Kobe.

LESPEDEZA VIOLACEA (L.) Pers. (Incl. L. prairea (Mack. and Bush) Britt.) (Plate XVIII, Figs. 1-3. Map 30)

Stems ascending or spreading, clustered, much branched, glabrate or appressed-puberulent. Stipules mostly 4-6 mm long. Leaflets petioled, ovate to elliptic, strigose or glabrate. Petaliferous flowers violet, in 4-6 flowered, filiform racemes; peduncles mostly exceeding subtending leaves. Keel usually exceeding other petals by about 1 mm. Apetalous flowers and fruits frequently abundant, in axillary clusters. Pod 4-6 mm long, strigose, about twice as long as petaliferous calyx.

L. violacea is common from central Texas northeast to New England. It has been infrequently reported from the southeastern states and appears rare on the southern coastal plain. The species occurs in all of the north-central states except the Dakotas and Minnesota. It is usually found in open, dry woodland and blooms in August or September.

Late season material of L. violacea which possesses entirely or predominantly axillary fruits (from apetalous flowers) is sometimes confused with L. intermedia or referred to L. acuticarpa Mack. and Bush. Usually such specimens possess the remnants of exerted peduncles (not found in L. intermedia) from which the sterile petaliferous flowers have fallen; also, L. violacea spreads, frequently with numerous, somewhat recurved branches, and bears dispersed leaves, while L. intermedia tends to be wand-like and closely leafy. Rarely, one encounters specimens in which the characters of L. violacea appear to be combined with those of other species. Such plants may possess included as well as exerted peduncles, and usually have narrower, hairier leaves than typical violacea. The type of L. acuticarpa Mack. and Bush (1902) is such a plant; its putative ancestry might be violacea x virginica.

See L. repens for comparative discussion of it and L. violacea.

Pierce (1939) and Young (1940) both reported a somatic 20 chromosomes for this species.

LESPEDEZA VIRGINICA (L.) Britt. (Plate XVIII, Figs. 4-6. Map 31)

Stems clustered, simple or branched at apex, erect, appressed-puberulent or less frequently hirsute, closely leafy. Leaf petioles various, the longer frequently exceeding 2 cm. Leaflets oblong to linear, strigose. Petaliferous flowers lavender in short-peduncled, 6-10 flowered racemes, appearing clustered in upper leaf axils and on short branches, densely glomerate at apex and giving stem a top-heavy appearance. Petaliferous calyx not more than half as long as pod. Fruits from apetalous flowers abundant.

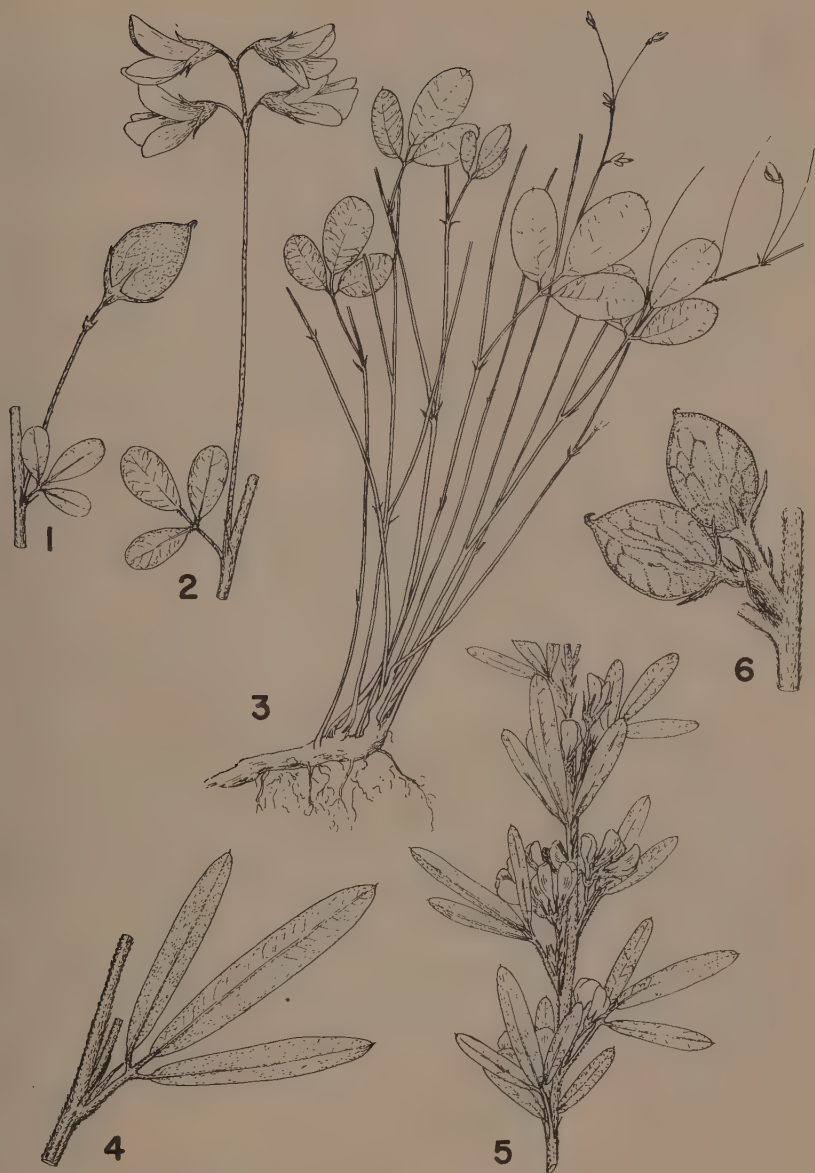


PLATE XVIII. LESPEDeza

Lespedeza violacea, 1. Fruit and subtending leaf $\times 2$. 2. Flower cluster and subtending leaf $\times 2\text{-}2/3$. 3. Habit, semi-diagrammatic $\times 2/3$.
L. virginica, 4. Leaf and stipule $\times 2$. 5. Flower-bearing upper portion of stem $\times 1\text{-}1/3$. 6. Mature fruit $\times 4$.

From east-central Texas, L. virginica ranges northeast to northern Illinois, southern Michigan and southern New England; it seems to occur throughout the southeastern states except for the outer margin of the coastal plain and Florida. In the north-central states area, the species is common only in the southern portion; it is apparently absent from Nebraska, the Dakotas and Minnesota (although reported from this state by Rydberg, 1932); it is found only in the southern extremities of Iowa, Wisconsin, and Michigan. In the southern United States, it is abundant, being especially typical of dry, impoverished, usually acid soils, in open woodlands or along roadsides, waste areas and abandoned fields.

In Indiana, Deam (1940) associates it with white and black oak ridges or post oak "flats" in dry, clayey soil, and states that "slightly acid soil or one low in fertility" is suggested.

Throughout most of its range, L. virginica does not come into bloom until late August or September; However, I have seen plants in Texas flowering by the middle of July.

For the most part, L. virginica is fairly consistent morphologically, but, as might be expected of a common and wide-ranging species, exhibits variational phases in several directions. Typical L. virginica possesses appressed, usually scant pubescence, but grades into a hairier series with spreading pubescence—by some authors termed forma deamii Hopkins, —which in turn, blends with L. stueveii angustifolia. However, most of the eastern state pubescent extremes do not possess the villous pods of L. stuevei, and I am considering them L. virginica; on the other hand, both forms occur among the southwestern (Arkansas, Texas, Oklahoma) representatives of these species. Occasional plants which appear like L. virginica, except for the presence of slightly broader leaflets and a few slightly exerted peduncles in the inflorescence, approach the form described by MacKenzie and Bush (1902) as L. acuticarpa and may represent intermediates with L. violacea. Another distinctive phenotype (or ecological form) has large, long petioled, widely spaced leaves on the main stem and in its extreme phase looks quite unlike typical L. virginica before flowering. Plants with unusually broad leaflets may be difficult to distinguish from L. intermedia, which is regarded by Schindler (1913) as a variety of L. virginica.

Pierce (1939) indicated the somatic chromosome number of Lespedeza virginica to be 22. Young (1940) made a number of determinations on several collections of the species and consistently obtained a gametic 10 or somatic 20. He discussed certain difficulties of determination that could account for this difference.

ONOBRYCHIS Mill.

Perennial herbs or spiny shrubs. Leaves odd-pinnate. Flowers in axillary spikes or racemes. Calyx with sharply pointed, subulate or lanceolate teeth. Petals usually purplish to white. Wings much shorter than standard. Stamens diadelphous. Pod one-seeded, indehiscent, usually flattened, often irregularly winged, with a thick sculptured pericarp.

Onobrychis, one of the major genera of the Hedysareae, comprises some 100 species, centering in eastern Europe and western Asia. The group appears related to Hedysarum, differing primarily in the one-seeded specialized form of the pod, and the reduced wing petals. One introduced species occurs sporadically in our range.

Literature

Gams (1923-24, 1487-1498).

ONOBRYCHIS VICIFOLIA Scop. (O. sativa Lam., O. onobrychis (L.) Korsten.) Sanfoin (Plate XIX, Figs. 1, 2)

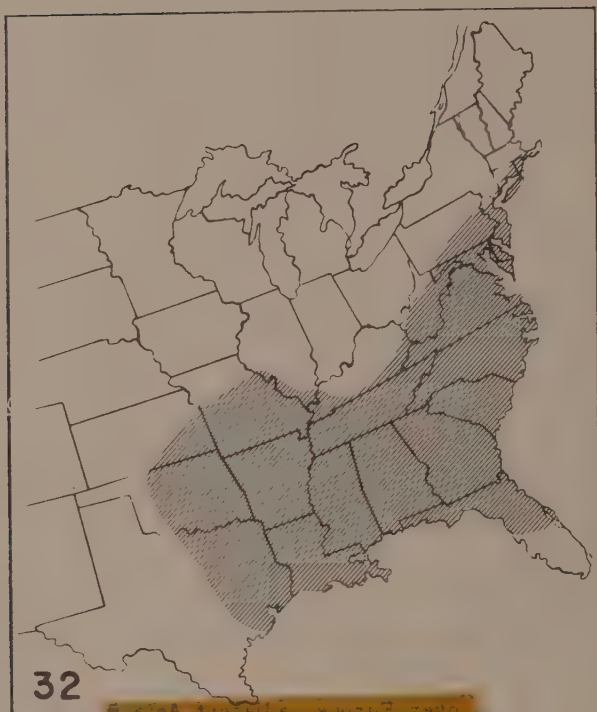
Stems numerous from a thick taproot, glabrate or sparsely hairy. Stipules brownish-membranous, lanceolate, conspicuously ensheathing stem base. Leaves petioled with 10-20 elliptic to oblong leaflets - those on rosetts blades broadly ovate. Racemes long-pedunculate, exceeding subtending leaves, the uppermost appearing terminal, closely-flowered. Calyx tube hirsute, campanulate, shorter than the awn-like, subulate teeth. Standard 8-12 mm long, rose with darker streaks, rarely white, striate, keel red. Pod flattened, semi-circular to ovate, 6-8 mm long, reticulate-ridged, marginally dentate. Seed elongate-oval, dull green, becoming brownish in age.

The sanfoin occurs over Europe, adjacent Asia and Mediterranean Africa. Since it has been widely distributed in connection with its employment as a forage legume, it is probable that its original range was much more restricted. The plant has been introduced into the United States several times for experimental purposes. However, it has not proved as satisfactory as other available forages, and is grown only on a rather limited scale. As an escape it has shown little tendency to persist or spread, except possibly in the Black Hills of South Dakota (Over, 1932), and is little mentioned in manuals. I have seen specimens from New Jersey, Missouri, South Dakota, Montana, Wyoming, and Colorado. The plant blooms in June or July.

O. viciifolia is a polymorphic species. Gams (1923-24) described 3 subspecies and numerous varieties. Senn (1938) reports a gametic (n) chromosome number of 11. Kunth (1908) described the pollination mechanism, a valvular arrangement essentially similar to that of Melilotus and Trifolium.

STYLOSANTHES Sw. Pencil-flower

Stipules fused to leaf petioles, ensheathing stem. Plants perennial. Leaves pinnately trifoliolate. Flowers in subterminal, axillary clusters, of two kinds, the petaliferous with a yellowish or orange corolla, the apetalous inconspicuous. Calyx tubular, slightly two-lipped. Stamens and petals arising from apex of



32. Stylosanthes biflora.

calyx tube. Stamens monadelphous, of two sets. Loment ovoid, woody, with one fertile joint, terminated by a curved or hooked beak.

This genus is represented in the southern United States and tropical America, Africa, and Asia. It is said, with reference to United States species of Stylosanthes, that seeds are set exclusively from apetalous flowers.

Literature

Fernald (1950, 928) eastern United States.

STYLOSANTHES BIFLORA (L.) BSP. (Incl. S. riparia Kearney) Pencil-flower. (Plate XIX, Figs. 3-5. Map 32)

Plants stiffly ascending; stem puberulent or bristly-hirsute. Free portion of stipules oblong-lanceolate, usually initially ciliate. Leaflets lanceolate (the lowermost broader), apiculate, to 4 cm in length, the upper sometimes marginally bristly. Pod puberulent when immature, lightly ribbed in maturity; apically beaked.

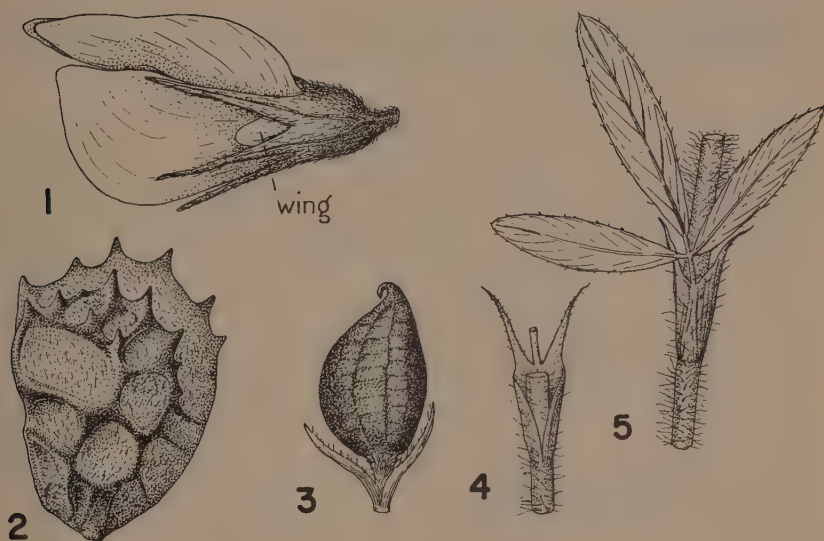


PLATE XIX. ONOBRYCHIS AND STYLOSANTHES

Onobrychis viciifolia, 1. Flower x 5. 2. Mature fruit x 5.

Stylosanthes biflora, 3. Mature fruit x 5. 4. Stipule x 2. 5. Leaf and stipule x 1-1/3.

The common pencil-flower is found throughout the southern and eastern states west to Oklahoma and Texas, north to central Missouri, southern Indiana and New Jersey.¹ It is ordinarily found in open woodlands, cut-over areas, or along roadsides, in acid or neutral soils. Deam (1940) in Indiana indicates its presence on open oak ridges. The plant may bloom at any time during the summer.

S. riparia Kearney is reported by Fernald (1950) from Missouri, Illinois, and Indiana in the north-central states region. It is said to differ from *S. biflora* in the possession of elliptic to ovate leaflets, and a symmetrically placed terminal beak on the pod, that of *S. biflora* being laterally offset. Specimens identifiable as *S. riparia* are most frequently found in woodlands in wet soil.

I am unable to maintain *S. riparia* as a distinct species. Leaflet width and shape are quite variable in *S. biflora*, and, so far as I can determine, there is no distinction between the forms with broader leaflets and similar plants which are said to be *S. riparia*. Likewise, the differences between fruits appears to be an artifact of observation. The terminal beak is usually offset more strongly along one horizontal axis of the fruit than

¹Var. *hispidissima* is reported from Arizona by Peebles and Kearney (1942) on the basis of a specimen in the Gray Herbarium said to be collected in "Arizona or New Mexico."

along the other at right angles to it. Hence, the degree to which the beak is, or is not symmetrically placed may depend on the angle from which it is viewed. Apparent beak position may also appear variable on immature fruits which have become flattened in drying.

Excluded Species and Synonyms

The specific names listed below largely fall into one of two categories, viz:

(1) Species reported for one or more of the north-central states, which are excluded on the basis that they do not represent a component of the native, naturalized or cultivated flora. Most of these are introduced perennial lespedezas which have been planted on a trial basis.

(2) Species reported (or binomials employed) in one or several recent manuals but which are relegated to synonymy on a taxonomic or nomenclatorial basis (also given as synonyms in foregoing text).

Desmodium acuminatum (Michx.) DC. This name has been displaced by the earlier published D. glutinosum (Willd.) Wood.

Desmodium bracteosum (Michx.) DC. Widely employed for D. cuspidatum (Willd.) Loud., but antedated by latter name.

Desmodium dillenii Darl. Included under D. paniculatum (L.) DC. on taxonomic grounds.

Desmodium glabellum (Michx.) DC. Treated as a variant of D. paniculatum (L.) DC.

Desmodium grandiflorum (Walt.) DC. Incorrectly employed by American authors for D. glutinosum. (Willd.) Wood.

Desmodium obtusum (Muhl.) DC. As employed by American authors, equivalent to D. ciliare (Willd.) DC.

Desmodium perplexum Schub. Largely synonymous with D. dillenii Darl., and included under D. paniculatum (L.) DC. on taxonomic grounds.

Hedysarum americanum (Michx.) Britt. Treated as a variety of H. alpinum L.

Hedysarum cinerascens Rydb. Submerged under H. boreale, Nutt. possibly deserving varietal status.

Hedysarum pabulare Nels. Regarded as synonymous with typical H. boreale Nutt.

Hedysarum philoscia Nels. Treated as a variety of H. alpinum L.

Hedysarum utahense Rydb. Included under H. boreale Nutt.

Lespedeza acuticarpa Mack. and Bush. Forms falling within the limits of this "species" appear to be intermediates (presumably hybrids) between members of the virginica-stuevei-intermedia triangle (see Fig. XIV) and L. violacea. These plants usually possess both exserted and short peduncles. The leaves are usually hairier and narrower than those of L. violacea with which they might otherwise be classified.

As indicated elsewhere, intermediate forms occur between several species of Lespedeza. For the most part these are unnamed. Those falling into the area said to be delimited by L. acuticarpa are less common than several other intermediate types, and certainly there is no evidence that they constitute a species in the biological sense.

- Lespedeza bicolor Turcz. This oriental, shrubby species is highly recommended in the southeastern states for wildlife and soil erosion plantings. It has been planted in Missouri and Kansas on a limited, experimental basis.
- Lespedeza formosa Koehne. An ornamental shrub, tabulated by Gates (1940) among Kansas cultivated legumes.
- Lespedeza frutescens (L.) Horn. This name has been widely employed for L. intermedia (Wats.) Britt. Linnaeus' Hedysarum frutescens has, however, been indicated to represent material of L. violacea (L.) Pers. (Schindler, 1913; Blake, 1924).
- Lespedeza japonica Bailey. Gates (1940) indicates that this ornamental, white-flowered species is cultivated in Kansas.
- Lespedeza longifolia DC. This name has been employed by several authors for the narrow-leaved extremes of L. capitata (L. capitata var. stenophylla Bissell and Fern.). Fernald (1941) has recently pointed out that the correct application of the name should be to narrow-leaved forms of L. hirta.
- Lespedeza neglecta (Britt.) Mack. and Bush. This plant is treated as L. stuevei var. angustifolia Britt. and is discussed under that species.
- Lespedeza prairea (Mack. and Bush) Britt. Originally described as a variety of L. violacea, this form was raised to specific rank by Britton. I am in accord with Blake (1924) and Schindler (1913) in being unable even to accord it nomenclatural status.
- Lespedeza sericea (Thunb.) Miq. Unfortunately this binomial must go into synonymy under L. cuneata (Dumont) Don as indicated under that species.
- Lespedeza texana Britt. A form of L. repens (L.) Bart.
- Meibomia. The various species of Desmodium are termed Meibomia in Small (1933), Britton and Brown (1913), Rydberg (1932), and other manuals. Meibomia is the earlier name, but Desmodium has been conserved in the International Rules of Nomenclature (Briquet, 1935).
- Stylosanthes riparia Kearney. Included under S. biflora (L.) BSP.

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¹ This book was published in three parts, the earlier two in 1838, the latter in 1840. Part of the treatment of the Leguminosae appeared in print in 1838, part in 1840--the break coming at page 360. We are citing the later date.

GROWTH OF CRAPPIES, BLUEGILL, AND WARMOUTH
IN LAKE AHQUABI, IOWA¹

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INTRODUCTION

Typically, artificial lakes pass through a cycle of good fishing in the early years of impoundment, fishing success generally decreasing after six to ten years. In the early years, the fish population has adequate food and room for rapid growth and expanding population. Thereafter, generally because of the inability of anglers to harvest the surplus production, the fish tend to become over-abundant in relation to food and space, and begin to grow more slowly (1, 20, 22, and others). Lake Ahquabi seems to have shown this typical cycle during its first 15 years of existence.

Lake Ahquabi is a shallow, artificial lake located six miles south of Indianola, Warren County, Iowa (Sec. 14, 32, R24W, T75N). The lake was impounded in 1935 in an area of Kansas drift, which is covered by loess, a wind blown silt. The Kansas drift and loess are underlain by bedrock of sandstone and shale (6).

The shape of the lake is roughly that of three arms, which extend north, south, and west; providing a relatively large amount of shore line. The lake has a surface area of 130 acres (8), and a maximum depth of 22 feet, which is found only on one restricted area. About 50 per cent of the lake varies from 7 to 15 feet in depth. The sides of the basin have a fairly steep gradient, although the slope varies greatly in different areas of the lake. Deltas have been formed by silt in the upper ends of the north and south arms, and also near the spillway.

Water lilies (Nymphaea odorata), coontail (Ceratophyllum demersum), arrowhead (Sagittaria latifolia var.), and floating leaf pondweed (Potamogeton natans) show luxuriant growth in the littoral zone. Small scattered stands of cattails (Typha latifolia) are also present. Submerged vegetation is all but absent in depths of 8 feet or more. Tom Moen (Biologist, State Conservation Commission: personal correspondence, May 20, 1953) indicates that this general vegetational condition has been present at least since 1947, with an apparent increase in vegetational growth in 1950 and 1951.

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Observations from varying sources indicate that the turbidity has been very high in the past. Moen (personal correspondence) recorded Secchi disk readings along with routine investigations of artificial lakes in 1947, 1949, 1950, and 1951. Only one observation was taken in the fall of each year, but the exceptionally low reading in 1947, 19 inches, supports the reports of high turbidity in previous years. Moen's readings for 1949, 1950, and 1951 were 42 inches, 60 inches, and 54 inches respectively. In July, 1951, the water level was raised about 1.5 feet. Following this, there was a reported decrease in turbidity, probably due to the settling out of colloidal silt particles by incorporation of shore vegetation (10, 11), better control of the watershed, immersion of strata being eroded by wave action and/or lack of excessive rain storms. Mean Secchi disk readings recorded by the author were 50 inches (range 30-68) in August and September, 1952, and 48 inches (range 35-72) in June, July, and August, 1953. Angling success reportedly improved as the turbidity decreased.

Investigations to determine what changes in the fish populations might have taken place were started in August, 1952. Data presented in this paper were collected in August and September, 1952, and June 15 to August 30, 1953.

MATERIALS AND METHODS

For the determination of growth, scales from 286 black crappie (Pomoxis nigromaculatus), 556 white crappie (Pomoxis annularis), 764 bluegill (Lepomis macrochirus), and 192 warmouth (Chaenobryttus coronarius) were used. In addition to the fishes used in this paper, largemouth bass (Micropterus salmoides), yellow perch (Perca flavescens), golden shiners (Notemigonis crysoleucas), green sunfish (Lepomis cyanellis), orangespotted sunfish (Lepomis humilus), northern black bullhead (Ameiurus melas), channel catfish (Ictalurus punctatus), and northern brook silversides (Labidesthes sicculus) were collected during the investigation.

Fish were collected by various methods, including hook and line, experimental gillnets, hoop nets, seines and wire traps. Most of the fish obtained by means of hook and line were sampled from the creels of fishermen, particularly in 1953 when an intensive creel census was taken. Hereafter, fish caught by methods other than hook and line will be referred to as the net sample.

Each type of gear was somewhat selective as to species and sizes of fish caught. The wire traps apparently selected larger young-of-the-year fish than did the seines (Table 1). Such a selection would be expected, since the traps had 1/2 inch mesh construction while the seine had 1/4 inch mesh (bar measure). The data are confounded, however, with possible changes in growth rates or different periods of hatching and/or with the fact that the seines could be used effectively only on the sand beach and the traps largely in the weedy areas.

Lengths at various annuli were computed from scale measurements using the Lee method (14, p. 121). The correction factors were computed by fitting the best straight line to the body scale relationship, as follows:

$$L = a + b S$$

Table 1. Mean total lengths, in inches, of young-of-the-year bluegill and crappies at Lake Ahquabi, 1952 and 1953, seine and wire trap samples. (Number of fish in sample in parentheses)

Species	Seine	Trap
Bluegill		
July, 1953	0.9 (172)	--
August, 1953	1.2 (189)	--
August, 1952	1.3 (76)	2.1 (10)
September, 1952	1.3 (53)	2.5 (13)
Black crappie		
June, 1953	1.2 (22)	--
July, 1953	1.5 (95)	--
August, 1953	2.0 (93)	3.2 (4)
August, 1952	--	2.7 (12)
September, 1952	--	3.2 (36)
White crappie		
July, 1953	1.6 (56)	--
August, 1953	1.7 (56)	--
August, 1952	--	2.8 (27)
September, 1952	--	3.1 (86)

where L is total length of fish, and S is scale radius. Then a is the correction factor to be used in computing lengths.

As a matter of convenience, since all measurements were recorded in inches or in grams, the condition factor, R , was used to determine the ponderal index (3). Calculations proceed on the basis of:

$$R = \frac{10W}{L^3}$$

where W is the weight in grams and L is the total length in inches. Conversion to the English "C" (using total length in inches and weight in pounds) is given by the relationship: $22.038R = C$.

Table 2. Relationship between standard and total length of crappies, bluegill, and warmouth, Lake Ahquabi

Species	Total length range inches	No. of fish	Formula for estimating standard length
Black crappie	2.2 - 9.1	195	$SL = 0.138 \text{ inches} + 0.7878 \text{ TL}$
White crappie	2.2 - 14.4	238	$SL = 0.132 \text{ inches} + 0.7572 \text{ TL}$
Bluegill	1.6 - 7.9	241	$SL = 0.15 \text{ inches} + 0.8071 \text{ TL}$
Warmouth	2.1 - 8.1	203	$SL = -0.17 \text{ inches} + 0.8536 \text{ TL}$

Total lengths, measured with the lobes of the caudal fin held together, are used throughout this report. Conversion formulas for converting total lengths to standard and fork lengths are given in Table 2. The statistical methods used in this study are mostly those of Snedecor (18).

GROWTH OF BLACK CRAPPIE

Adult black crappie were not very abundant in Lake Ahquabi in 1952 and 1953. There is evidence to be discussed later that they may be increasing in abundance.

Lengths of the black crappie at various years were computed from scale measurements using the Lee method (14). A correction value of 1.8 inches was used since this length was the intercept of the straight line best fitting the body-scale relationship (Fig. 1).

The growth of black crappie in Lake Ahquabi (Table 3) is somewhat

Table 3. Growth of black crappie, Lake Ahquabi

(Total length in inches and weight in grams)

Year Class	Yr. Col- lected	No. Ex- amined	Mean length at cap- ture	Mean calculated length at annulus				
				1	2	3	4	5
1953	1953	92	2.0					
1952	1952	48	3.1					
	1953	48	5.4	3.4				
1951	1952	1	4.9	2.8				
	1953	7	7.7	3.0	6.2			
1950	1953	11	8.3	3.4	5.6	7.4		
1949	1952	8	7.7	3.4	5.5	6.7		
	1953	65	8.6	3.3	5.4	6.6	7.9	
1948	1952	4	8.2	3.6	4.9	6.2	7.3	
	1953	2	10.3	3.4	5.7	6.9	8.0	9.7
Mean calculated length				3.3	5.5	6.7	7.9	9.7
Mean annual length increment				3.3	2.2	1.3	1.3	1.7
Equivalent weight*				7.2	35.7	65.5	111.6	212.7
Weight increment*				7.2	28.5	31.8	48.2	96.7
Equivalent standard length in millimeters				70	113	137	162	198

*Log W = -0.7737 + 3.1430 Log L

slower than that in other Iowa waters which have been studied (4, 15). At the present rate of growth, the black crappie reach creel size during their third and fourth summer of life and reach a weight of 1/4 pound at about eight inches. It was thought that the size selectivity of angling or trapping might result in differences in growth rates in the two samples. Growth rates of the 1953 netting and creel samples were not found to be significantly different at the 0.05 probability level (Table 4). The samples were therefore combined for analysis of the growth.

The length-weight relationship, based on 82 fish from the 1953 net sample only, was determined by converting the measurements into logarithms and fitting a straight line to the data by the least squares method (Fig. 2). The relationship is described by the formula:

$$\text{Log } W = 0.7737 + 3.1430 \text{ Log } L$$

where W is the weight in grams and L is the length in inches.

The slope of the line, 3.1430, indicates that the weight of the fish increases at a greater rate than the cube of the length (standard error of regression slope, $S_b = 0.0426$; $t_0 = 3.36$, 80 d.f.). The longer fish are thus more than proportionately heavier than the shorter fish, which is also shown by the increasing coefficient of condition in older age groups (Table 5). The 95 per cent prediction interval for given lengths (19, p.120) was also plotted in Fig. 2. The prediction interval is interpreted that we are 95 per cent confident that this interval will contain a single weight, given length.

The condition factor, R, of the black crappie (Table 5) varies from 2.171 in age group I to 2.311 in age group IV. The equivalent range of "C" values (47.8 to 50.9) is considered to be average according to Minnesota standards (2).

Table 4. Tests of significance between calculated growth of creel and net samples of black crappie from Lake Ahquabi, 1953 (total length in inches).

Age group		Number examined	Calculated t_0 and standard error for mean length at annulus							
			1		2		3		4	
			SE	t_0	SE	t_0	SE	t_0	SE	t_0
III	Creel	4								
	Net	7	.143	1.19	.264	2.12	.293	.85		
IV	Creel	43								
	Net	22	.119	.08	.123	1.38	.112	.45	.099	1.11

None of the t_0 values are significant at the 95 per cent level.

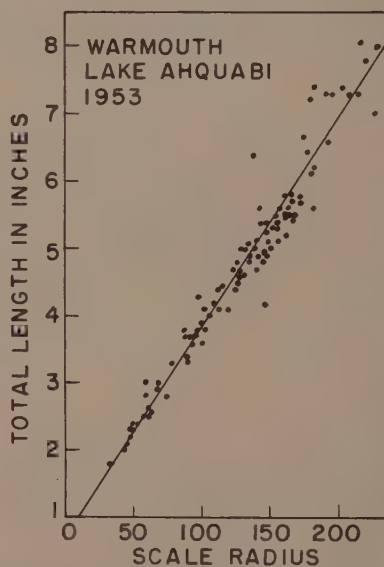
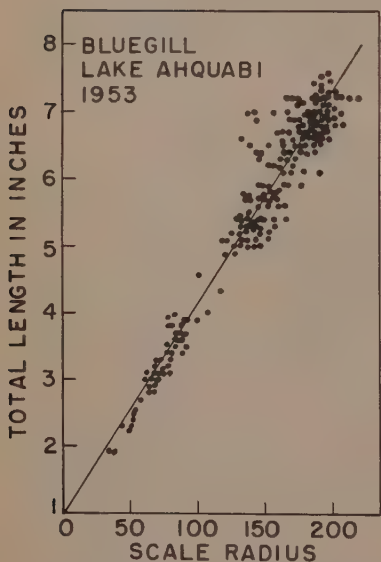
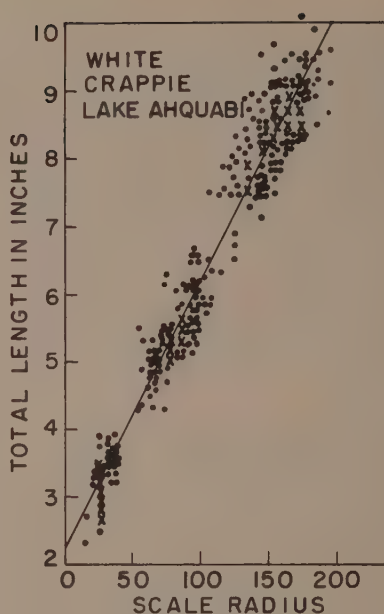
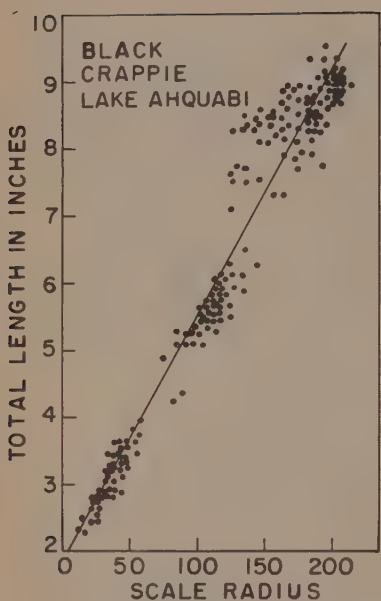


Fig. 1. Body-scale relationships of black crappie, white crappie, bluegill, and warmouth from Lake Ahquabi, Iowa.
(124)

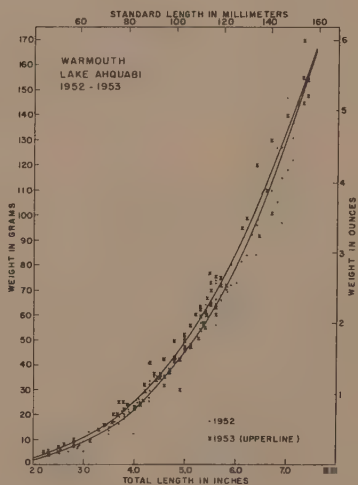
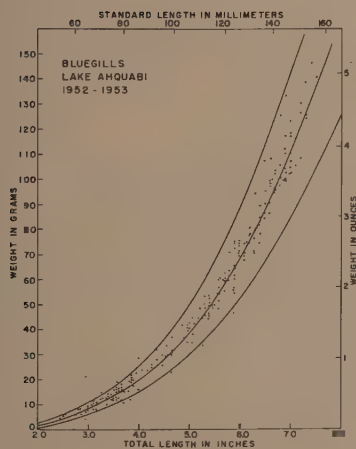
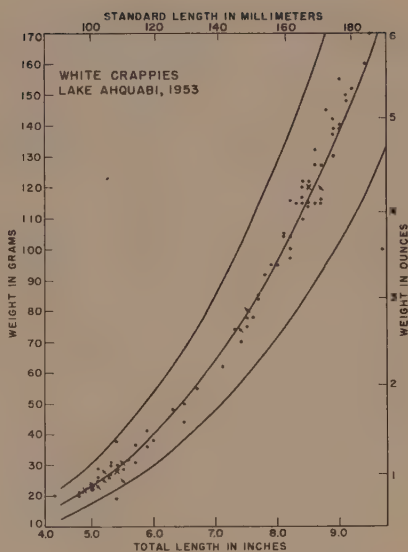
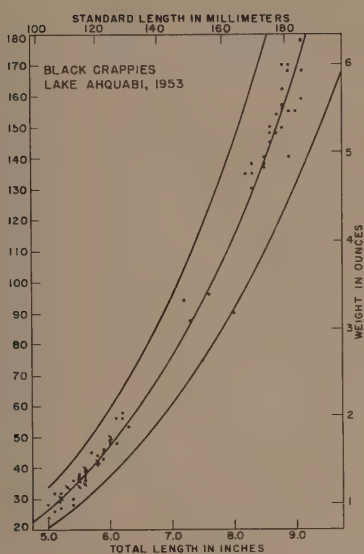


Fig. 2. Length-weight relationships of black crappie, white crappie, bluegill, and warmouth from Lake Ahquabi, Iowa.
(Formulae, pp. 123, 127, 129, 132).

Table 5. Mean weight, coefficient of condition, R, and equivalent "C" for black crappie from Lake Ahquabi, 1953 (weight in grams)

Age group	Number examined	Mean weight at capture	Mean R	Equivalent C (T.L.)*
I	46	39	2.171	47.8
II	5	95	2.297	50.6
III	8	129	2.245	49.5
IV	23	153	2.311	50.9

*22.038 R = C (T.L.)

Table 6. Growth of white crappie, Lake Ahquabi
(Total length in inches and weight in grams)

Year Class	Yr. Col-lected	No. Exam-ined	Mean length at capture	Mean calculated length at annulus			
				1	2	3	4
1953	1952	52	1.8				
1952	1952	115	3.1				
	1953	159	5.4	3.6			
1951	1952	2	5.3	3.3			
	1953	19	7.7	3.4	6.1		
1950	1952	1	7.5	3.7	5.5		
	1953	9	8.6	3.9	6.0	7.6	
1949	1952	55	7.9	3.6	5.5	6.6	
	1953	139	8.6	3.6	5.4	6.4	7.7
1948	1952	5	8.9	3.3	5.1	6.9	8.0
Mean calculated length				3.6	5.5	6.5	7.7
Mean annual increment				3.6	1.9	1.1	1.3
Equivalent weight*				8.5	30.8	51.2	85.8
Weight increment*				8.5	22.3	22.1	37.0
Equivalent standard length in millimeters				73	109	128	127

*Log W = -0.7682 + 3.0477 Log L.

GROWTH OF THE WHITE CRAPPIE

Creel census in 1953 disclosed that the white crappie contributed about 47 per cent of the angler's catch during the summer. Under such conditions the growth of white crappie is particularly important in the management of Lake Ahquabi.

The body-scale relationship of the white crappie was obviously different from that of the black crappie (Fig. 1). A straight line with an intercept of 2.2 inches gave the best fit and this value was used as the correction value in computing growth.

Growth calculations for the white crappie (Table 6) are based only on fish from the net samples, both in 1952 and 1953. With the present growth rate, the white crappie reach creel size, over 7.5 inches, sometime during their third and fourth summers of life, and reach a weight of 1/4 pound during their fourth summer of life. The growth of Lake Ahquabi white crappie appears to be slightly slower than that of other Iowa waters (4,15).

The length-weight relationship (Fig. 2) was computed from a random sample of 101 fish from the 1953 net sample only and is described by the equation: $\log W = -0.7682 + 3.0477 \log L$.

The slope of the line, 3.0477, does not differ significantly from 3.0 ($S_b = 0.042$; $t_0 = 1.14$, 99 d.f.).

The condition factors of the white crappie (Table 7) are consistently lower than those of the black crappie.

The slopes of the length-weight relationships of the black and white crappies are not significantly different (Table 8). The test between adjusted weight means, however, is highly significant, indicating that the black crappie have a greater weight at the same unit length than the white crappie. In most populations black crappie are noticeably heavier than white crappie.

Table 7. Mean weight; coefficient of condition, R; and equivalent "C" for white crappie from Lake Ahquabi, 1952 and 1953 (weight in grams)

Age group	Number examined	Mean weight at capture	Mean R	Equivalent C* (T.L.)
<u>1952</u>				
I	2	24	1.57	34.59
II	1	78	1.85	40.77
III	43	89	1.87	41.12
IV	5	147	1.74	38.35
<u>1953</u>				
I	149	39	1.81	39.82
II	17	83	1.84	40.53
III	8	118	1.93	42.45
IV	134	127	1.94	42.69

*22.038 R = C (T.L.)

Table 8. Tests of significance between the length-weight relationships of black and white crappies, Lake Ahquabi, 1953

Species	d.f.	b's	S_b^2	$\sqrt{.0036} = .0600$			
White	100	3.0477	.0018	$t_0 = \frac{.0953}{.0600} = 1.588, 181 \text{ d.f.}$			
Black	81	3.1430	.0018				

Source	d.f.	Σx^2	Σxy	Σy^2	Errors of Estimate		
					d.f.	SS	MS
Between Species	1	.0048	-.0195	.0801			
Within Species	181	1.7543	5.4137	17.0034	180	.2969	.0016
Total	182	1.7591	5.3942	17.0835	181	.5424	
Differences for testing adjusted means					1	.2455	.2455
$F = \frac{.2455}{.0016} = 153.44$							

The growth rates of the two crappies are quite similar except that the black crappie tend to be a little larger in the 3rd and 4th year. Both species of crappie of Lake Ahquabi show the short life span and fluctuations of abundance which are apparently typical of the species (7, 12, 19, 21).

GROWTH OF THE BLUEGILL

Creel census during the summer of 1953 revealed that the bluegill constituted 46.8 per cent of the sample catch. Unlike the crappies, the bluegill of Lake Ahquabi show a steady abundance from year to year and hence are the mainstay of the fishery. In consequence, the growth of the bluegill in Lake Ahquabi is of prime importance.

The body-scale relationship was determined for both the 1952 and 1953 sample. A straight line was fitted by the least squares method for both years and resulted in the following equations:

For 1952: $Y = 1.05 - 0.0386 X$ (based on 434 fish)

For 1953: $Y = 1.03 - 0.0313 X$ (based on 214 fish)

where Y is the anterior scale length x 50 and X is the total length of the fish in inches. As the intercepts of both regressions are much the same, a correction of 1 inch was used in the growth computations according to the Lee method (14, p. 121).

The greatest annual length increment occurs during the first year of life, declining somewhat steadily thereafter (Table 9). In 1953 the bluegill reached creel size, over 6 inches, during their fourth summer of life. The bluegill reach a weight of 1/4 pound in about five years. The growth of bluegill in Lake Ahquabi is somewhat slower than that in other Iowa waters (15, 17).

Table 9. Growth of bluegill, Lake Ahquabi

(Total length in inches and weight in grams)

Year Class	Yr. Collected	No. Examined	Mean length at capture	Mean calculated length at annulus				
				1	2	3	4	5
1953	1953	375	1.0					
1952	1952	129	1.3					
	1953	49	3.2	2.3				
1951	1952	274	3.6	1.7				
	1953	59	5.4	1.7	4.0			
1950	1952	24	4.6	1.8	3.3			
	1953	9	6.3	2.2	3.8	5.1		
1949	1952	53	5.8	2.2	3.6	4.8		
	1953	68	6.8	2.1	3.7	4.8	5.9	
1948	1952	70	6.2	1.9	3.6	4.6	5.4	
	1953	29	6.9	2.0	3.5	4.5	5.3	6.3
Mean calculated length				1.9	3.7	4.7	5.6	6.3
Mean annual increment				1.9	1.7	1.1	1.0	1.0
Equivalent weight*				2.0	15.7	32.7	56.1	80.5
Weight increment*				2.0	13.3	18.3	25.5	33.2
Equivalent standard length in millimeters				43	80	100	119	133

*Log W = -0.5526 + 3.0757 Log L

The length-weight relationship was determined for both 1952 and 1953 based on random samples of 88 fish in 1953 and 141 fish in 1952. The manner of computation was the same as that previously outlined and resulted in the following equations:

For 1952: $\log W = -0.5307 + 3.0419 \log L$ For 1953: $\log W = -0.5804 + 3.1123 \log L$

Analysis of covariance (Table 10) indicates that there is no significant difference between the two length-weight regressions. A pooled regression was therefore computed where: $\log W = -0.5526 + 3.0757 \log L$.

The slope indicates the weight increases at a rate slightly more than the cube of the length ($S_b = 0.0316$; $t_0 = 2.40$, 227 d.f.).

The condition factors (Table 11) of the bluegill seem to indicate only a slight tendency to increase with the age groups. They are higher than those for either the black or white crappies from Lake Ahquabi. The C values compare favorably with those listed by Ruhr (17) and are within the average range for Minnesota (2).

Table 10. Analysis of covariance to test the differences between the length-weight regressions of the bluegill in 1952 and 1953.

Test of regression coefficients:

Source	Errors of estimate		
	d.f.	SS	MS
Average within years	226	0.8165	
Deviations from individual regressions	225	0.8126	0.0036
Differences between regression coefficient	1	0.0039	0.0039

$$F = \frac{0.0039}{0.0036} = 1.08, 1 \text{ and } 225 \text{ d.f.}$$

Test of adjusted means:

Source	d.f.	Σx^2	Σxy	Σy^2	Errors of estimate		
					d.f.	SS	MS
Total	228	3.5925	11.0494	34.8011	227	.8166	
Between years	1	.0216	.0701	.2270			
Within years	227	3.5709	10.9793	34.5741	226	.8165	.0036
Differences for testing adj. means					1	.0001	.0001

$$F = \frac{.0001}{.0036} = .0278, 1 \text{ and } 227 \text{ d.f.}$$

Table 11. Mean weight, coefficient of condition, R, and equivalent "C" for bluegill, Lake Ahquabi, 1952 and 1953 (weight in grams)

Age group	Number examined	Mean weight at capture	Mean R	Equivalent C (T.L.)*
<u>1952</u>				
I	213	15.97	3.10	68.32
II	19	30.84	3.30	72.73
III	36	62.31	3.16	69.64
IV	40	83.30	3.22	70.96
<u>1953</u>				
I	31	12.81	3.05	67.21
II	58	52.43	3.24	71.40
III	7	87.57	3.32	73.17
IV	67	99.79	3.23	71.18
V	26	115.19	3.44	75.81

*22.038 R = C(T.L.)

GROWTH OF THE WARMOUTH

Very few warmouth are caught by Lake Ahquabi fishermen, due either to their apparent relative scarcity in Lake Ahquabi or to their habit of remaining in the densely weeded areas of the lake.

Body-scale relationships were determined for 1952 and 1953 by fitting a straight line to the data with the least squares method (Fig. 1). The relationships are expressed for the two years by the following equations:

For 1952: $Y = 0.7824 - 0.0404 X$ (based on 92 fish)

For 1953: $Y = 0.7952 - 0.0305 X$ (based on 100 fish)

where Y is the total length of the fish in inches and X is the anterior scale radius x 50 in millimeters. In computing growth an intercept correction of 0.8 inches was used both years.

The growth of the warmouth in Lake Ahquabi (Table 12) is similar to that of the bluegill and slightly less than that of the crappies. The greatest annual length increment occurred during the first year of growth in 1952 and during the second year of growth in 1953. The growth increment is somewhat greater in the later years of life than that of the crappies or bluegill in Lake Ahquabi.

Table 12. Growth of warmouth, Lake Ahquabi

(Total length in inches and weight in grams)

Year Class	Yr. Collected	No. Examined	Mean length at capture	Mean calculated length at annulus				
				1	2	3	4	5
1952	1953	33	3.1	1.8				
1951	1952	48	3.7	1.7				
	1953	48	5.1	1.7	4.0			
1950	1952	19	5.6	1.8	3.6			
	1953	6	6.0	1.8	3.1	4.9		
1949	1952	23	6.6	1.8	3.3	5.0		
	1953	12	7.2	1.9	3.4	4.7	6.6	
1948	1952	2	6.6	1.7	3.1	4.8	5.9	
	1953	1	7.8	1.5	2.8	4.2	5.9	7.1
Mean calculated length				1.7	3.6	4.9	6.5	7.1
Mean annual length increment				1.7	1.9	1.6	1.8	1.2
Equivalent weight*				1.4	15.5	41.7	103.1	136.8
Weight increment*				1.4	14.1	30.0	66.6	61.2
Equivalent standard length in millimeters				33	74	102	137	150

*Log W = - 0.5918 + 3.2044 Log L

Table 13. Mean weight, coefficient of condition, R, and equivalent "C" for the warmouth, Lake Ahquabi, 1952 and 1953 (weight in grams).

Age group	Number examined	Mean weight at capture	Mean R	Equivalent C (T.L.)*
<u>1952</u>				
I	40	18.85	3.41	75.15
II	14	68.93	3.71	81.76
III	18	106.61	3.70	81.54
IV	2	105.50	3.53	77.79
<u>1953</u>				
I	26	17.27	4.07	89.69
II	42	55.67	3.87	85.29
III	6	91.17	4.06	89.47
IV	12	154.83	4.00	88.15
V	1	204.00	4.30	94.76

* $22.038 R = C (T.L.)$

The growth of warmouth in Lake Ahquabi appears to be slower than that reported for Red Haw Lake, Iowa, (16) particularly in the later years of life.

Length-weight relationships, determined in the same manner as for the other species, yielded the following equations:

For 1952: $\log W = -0.5918 - 3.2044 \log L$ (based on 74 fish)

For 1953: $\log W = -0.3952 - 2.9873 \log L$ (based on 87 fish)

A "t" test between the regression coefficients of the 1952 and 1953 samples (Table 14) is sufficient to show that the two regressions are not the same.

The warmouth apparently were heavier for their length in 1953 than in 1952 (Fig. 2), a situation which is also evident from a comparison of the condition factors (Table 13). The change in slope of the length-weight relationships is such as might be expected with an improvement of "condition" which would have a greater proportional effect on small than on large fish.

The condition factors of the warmouth are considerably greater than those of the crappies, depicting the more stocky appearance of the warmouth.

The 1952 length-weight formula was used in computing weights and weight increments (Table 12) since it probably more nearly represents the relationship during the years under study.

POPULATION CHANGES

A comparison of relative numbers of the various age groups of black and white crappies captured in 1953 (Table 15) suggests a possible shift in species composition of the population. Gillnet collections have been

Table 14. Test of significance for the difference between regression coefficients of the length-weight relationship, warmouth, Lake Ahquabi, 1952 and 1953

year	d.f.	b	S_b^2	$\sqrt{.0045} = 0.67$
1952	73	3.2044	.0030	
1953	86	2.9873	.0015	$t_0 = \frac{.2171}{.067} = 3.24^{**}$

**Significant at the 0.01 per cent level.

Table 15. Frequency of different age groups of black and white crappies caught in wire traps, hoop nets and seine, Lake Ahquabi, 1953 (Numbers represent total catch).

Age group	Black crappie	White crappie
0	211	112
I	406	143
II	4	19
III	7	8
IV	22	124

left out of this comparison because the black crappie were observed to be deeper in proportion to the length than white crappie and hence black crappie may be less susceptible to capture in the gillnets. In 1953, gillnets captured only 2 age group I black crappie while capturing 18, 1, and 15 white crappie of age groups I, III, and IV, respectively. Wire traps, hoop nets, and seines are assumed to be nonselective for either species. Comparison of catches in 1953 reveals that possibly the black crappie of age groups 0 and I were more numerous than white crappie of the same age, and that white crappie of age group IV were more numerous than black crappie of the same age. This possible change in species composition is particularly interesting as there have been many references to the fact that white crappie tend to be more abundant than black crappie in the muddy, turbid waters (5, 8, 9, 13). Lake Ahquabi is understood to have been very turbid in 1947 and earlier years, clearing considerably in 1951 to 1953 (mean Secchi disk reading in 1953 was 48 inches).

The possible changes in growth rate are best observed by plotting the annual increment of growth in relation to age and the year in which it occurred (Table 16). The rather sharp and consistent increase of the annual growth increment in all age groups of all species between 1951 and 1952 is apparent. Further, the growth increment in 1951 and earlier years is more or less constant, and in most cases less than that of 1952.

Table 16. Annual total length increments in inches of black and white crappies, bluegill and warmouth collected in Lake Ahquabi (number of fish in parentheses) 1952-53

Species and Year of Life	Year in which growth occurred				
	1952	1951	1950	1949	1948
<u>Black</u>					
<u>crappie</u>					
1	3.4 (48)	3.0 (8)	3.4 (11)	3.3 (73)	3.5 (6)
2	3.2 (7)	2.2 (11)	2.1 (73)	1.6 (6)	
3	1.8 (11)	1.2 (73)	1.3 (6)		
4	1.3 (65)	1.1 (6)			
5	1.7 (2)				
<u>White</u>					
<u>crappie</u>					
1	3.6 (159)	3.4 (21)	3.9 (10)	3.6 (194)	3.3 (5)
2	2.7 (19)	2.1 (10)	1.8 (194)	1.7 (5)	
3	1.6 (9)	1.0 (194)	1.8 (5)		
4	1.3 (139)	1.1 (5)			
<u>Blue-</u>					
<u>gill</u>					
1	2.3 (49)	1.7 (323)	1.9 (33)	2.1 (121)	1.9 (99)
2	2.3 (59)	1.5 (33)	1.5 (121)	1.6 (99)	
3	1.3 (9)	1.2 (121)	1.0 (99)		
4	1.1 (68)	0.8 (99)			
5	1.0 (29)				
<u>Warmouth</u>					
1	1.8 (33)	1.7 (96)	1.8 (25)	1.8 (35)	1.6 (3)
2	2.2 (48)	1.7 (25)	1.5 (35)	1.4 (3)	
3	1.8 (6)	1.6 (35)	1.6 (3)		
4	1.9 (12)	1.3 (3)			
5	1.2 (1)				

Statistical analysis is somewhat complicated by the rather large discrepancies in size of samples used to compute the various increments. Mr. D.V. Huntsberger, of the Iowa State College Statistical Laboratory, pointed out a technique whereby a transformation of the following nature is used:

$$Y_i = \frac{X_{i1} - X_{i2}}{\sqrt{\frac{1}{n_{i1}} + \frac{1}{n_{i2}}}}; \text{ where}$$

$$\sqrt{\frac{1}{n_{i1}} + \frac{1}{n_{i2}}}$$

Y_i is the transformed value of the difference, X_{i1} and X_{i2} are the two original values which have been paired and n_{i1} , n_{i2} are the number of observations associated with each respective pair. The transformed values

of difference will now all have the same variance. Computation may now proceed by pairing the increments of 1952 and 1951 for the same year of life in each case and testing the mean difference between 1952 and 1951 as outlined in Snedecor (18, p. 44). As the test is relatively inefficient, insignificant results may be misleading. Statistically significant results, however, are strongly indicative of true changes.

The mean difference between 1952 and 1951 for all species combined was highly significant, showing a definite acceleration of growth in 1952. Tests made for each species separately, revealed significant differences (black crappie, $t_0 = 3.68$, 3 d.f.; white crappie $t_0 = 6.87$, 3 d.f.; bluegill, $t_0 = 3.64$, 3 d.f.) with the exception of the warmouth ($t_0 = 2.67$, 3 d.f.). A partial explanation of this may lie in the fact that the warmouth inhabits the weedy areas of the lake more than the other species and the environmental changes of the lake in 1952 might not have affected this area to the extent that it did the rest.

There is an indication (Table 17) that the growth of the crappies, but not the bluegill, may have slowed again in 1953. Further data must be obtained before this can be ascertained with any certainty, however.

Table 17. Length increment in inches from last annulus to time of capture in August, Lake Ahquabi

	Age I		Age II		Age III		Age IV	
	1952	1953	1952	1953	1952	1953	1952	1953
Black crappie	--	--	--	--	1.5	1.2	1.3	1.0
White crappie	--	--	--	--	1.9	1.4	1.5	1.3
Bluegill	1.7	1.1	1.4	1.6	1.0	1.6	0.6	0.7
Warmouth	1.2	2.0	1.8	1.4	1.5	--	--	0.8

The causes of the evident changes in the population could be numerous. The two most apparent changes of environment in Lake Ahquabi were the reduction of turbidity in the last few years and the increase in the volume of the lake in 1951. Also, the fishing success has apparently increased steadily in 1951, 1952, and 1953.

SUMMARY

1. Fishery investigations were started on Lake Ahquabi in the fall of 1952, continuing over August and September, 1952, and June, July, and August, 1953, to determine what possible changes in the fish population might have accompanied the noted changes in environment.

2. Growth data for the white and black crappies, bluegill, and warmouth have been analyzed and are presented in the paper.

3. A definite acceleration of growth was found to have occurred in 1952, accompanying a decrease in turbidity and increase in volume of the lake.

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EFFECT OF FLUORESCENT AND INCANDESCENT LIGHT ON
TEMPERATURES IN PHOTOPERIODIC CHAMBERS¹

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INTRODUCTION

Artificial light has frequently been used in greenhouse work either to supplement natural daylight or extend the daylength in photoperiodic experiments. The use of such light influences light intensity and light quality, both of which are important factors in plant growth. Light quality is particularly affected by the light source and may differ appreciably from that of natural daylight.

It often has been assumed that incandescent lamps cause considerable heating. Because of this heating, a temperature effect, as well as the photoperiodic effect, may be introduced into the results.

Incandescent lamps, emitting a continuous spectrum with maximum radiation in the near infrared at about 10,000 Å (Withrow and Withrow, 6) are relatively rich in red and weak in blue light. A 500-watt incandescent light source radiates 12 per cent of the input wattage in the visible spectrum and 70 per cent in the infrared. The remaining 18 per cent is dissipated largely as heat by convection and conduction.

Fluorescent lamps, which emit a continuous spectrum with maximum radiation at about 5,800 Å, have high line spectra at 4,050, 4,350, and 5,460 Å. A 40-watt daylight fluorescent lamp emits approximately 20 per cent of the input wattage in the visible spectrum and 25 to 30 per cent in the infrared. Over 50 per cent of the input wattage is dissipated as heat by convection and conduction.

Gelin and Burström (1) have recommended fluorescent light for "climatic chambers." Moss and Loomis (3) and Loomis (2) have shown the absorption of light by a leaf is over 90 per cent from 4,000 to 4,500 Å, decreases to about 60 per cent at 5,500 Å, increases to 90 per cent at 6,800 Å, and then decreases to almost 5 per cent at 10,000 Å. At 30,000 Å absorption has increased to almost 100 per cent. The absorption of light by the leaf is much greater in the wave lengths emitted by the fluorescent source than the incandescent source.

The objectives of this study were to evaluate the leaf and air temperature differences under incandescent and fluorescent lights of different intensities and to evaluate the difference between these two light sources.

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The study was supplemental to the main purpose of the experiment which was to study the effect of long and short day lengths on the flowering of various strains of sweet clover.

MATERIALS AND METHODS

Hubam sweetclover plants, about 13 weeks old, were used in these experiments. They were grown in light chambers 28" x 35" x 48" with a black light-tight curtain on one side. The curtain was raised about 0800 each day, to permit sunlight to enter the chamber, and lowered at 1700. Greenhouse temperatures varied from 68° to 72°F, except at midday when natural sunlight occasionally raised the temperature to 90° to 100°F.

Various supplemental light sources were used. These consisted of: (1) one 20-watt daylight fluorescent lamp and one 20-watt white fluorescent lamp (a source frequently used in the greenhouse), (2) two 20-watt daylight fluorescent lamps and three 20-watt white fluorescent lamps, (3) one 100-watt clear incandescent lamp, and (4) one 150-watt clear incandescent lamp.

Temperature measurements, both on the leaf surface and in the air, were made using 30-gauge, enamel-coated, cotton-wrapped copper-constantan thermocouples. The thermocouples were formed by twisting the two bared wires together, heating them in an alcohol flame, and touching them with solder. The couples were then trimmed to a short, sharp, bright point. The temperatures of the thermocouples were determined with a Brown electronic recording potentiometer which recorded 16 different thermocouple readings in 80 seconds. Leaf temperatures were recorded by threading the thermocouples into the sweetclover leaves at varying distances from the light source. If the thermocouples are changed daily and the sensitive tip kept in contact with fresh tissue, little error should be encountered because of tissue injury. Waggoner and Shaw (4) believed that temperature readings made in this way closely approximate leaf temperatures. Since shading may produce undesirable effects in small photoperiodic chambers, comparable air and leaf temperature measurements were made with unshielded thermocouples. Although unshielded thermocouples do not measure "true" air temperature, they give a close approximation of it, except possibly when very close to the light source.

RESULTS AND DISCUSSION

The leaf temperatures for the extremes of light intensity used are presented in Figs. 1 and 2. Under the 40-watt fluorescent light source (one 20-watt daylight fluorescent lamp and one 20-watt white fluorescent lamp) leaves 12 inches from the light source were about 5°F warmer than those 33 inches from the source. Under the 150-watt incandescent lamp this difference was about 10°F.

When 100-watt incandescent and 100-watt fluorescent light sources (two 20-watt daylight fluorescent lamps and three 20-watt white fluorescent lamps) were used and the curtains were closed, leaves 2 inches from the incandescent lamp were 10° to 15°F warmer than leaves 2 inches from the fluorescent lamps. This is probably a direct heating effect from the hot incandescent lamp. Thermocouples placed in leaves, 12, 24, and 36

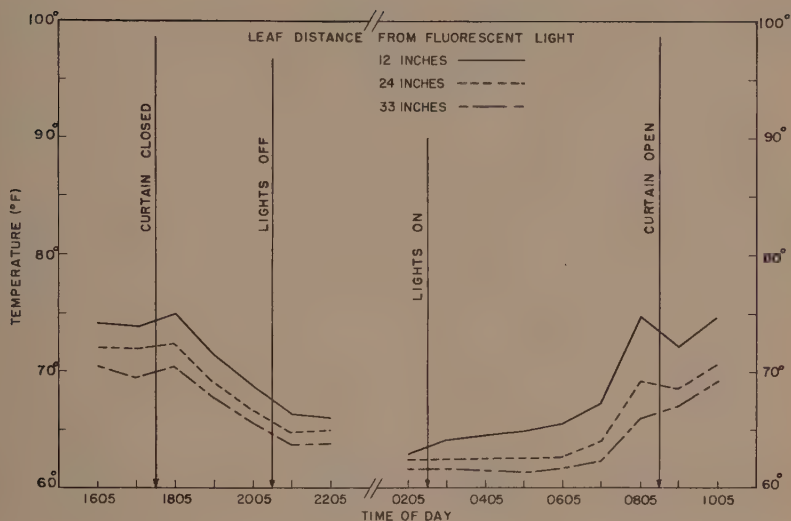


Fig. 1. Leaf temperatures at varying distances from a 40-watt fluorescent light source at different times during the day.

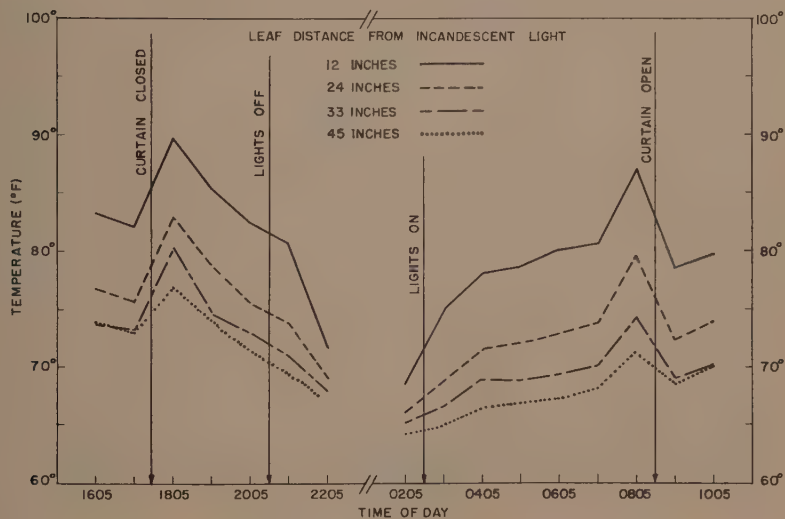


Fig. 2. Leaf temperatures at varying distances from a 150-watt incandescent light source at different times during the day.

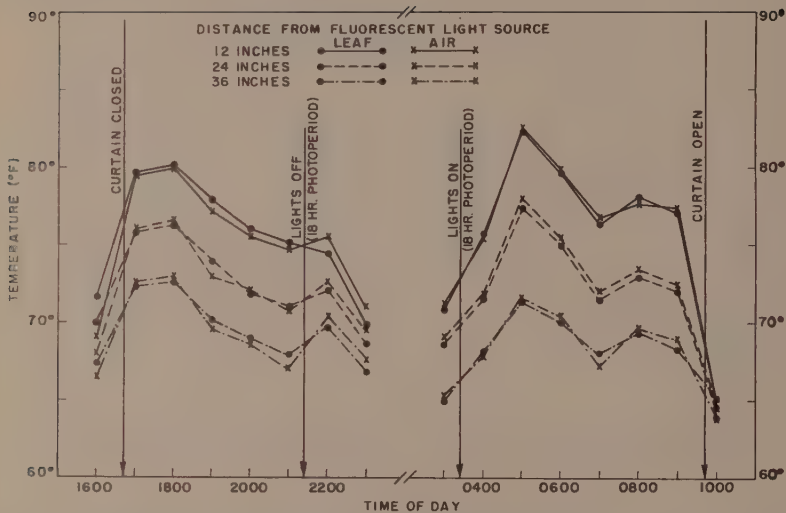


Fig. 3. Leaf and air temperatures at varying distances from a 100-watt fluorescent light source at different times during the day.

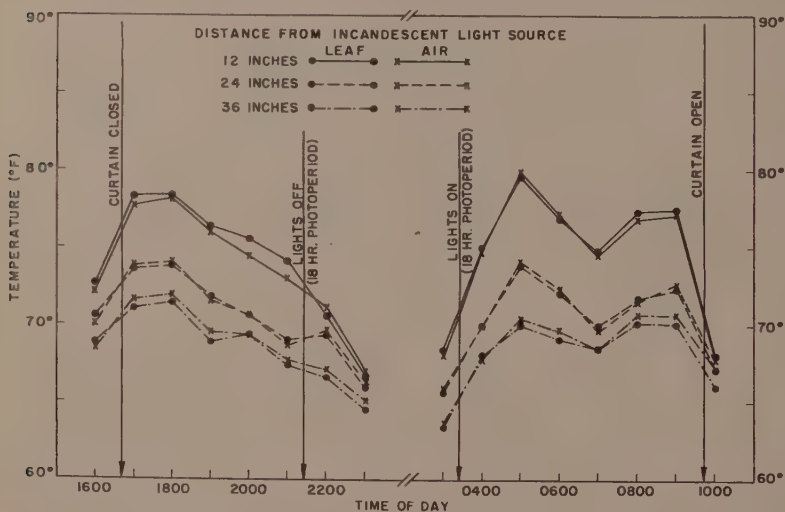


Fig. 4. Leaf and air temperatures at varying distances from a 100-watt incandescent light source at different times during the day.

inches from these light sources, showed that leaves exposed to incandescent light were about the same temperature to slightly cooler than leaves exposed to fluorescent lights at the same distances. In all cases, leaves farthest from the light source were the coolest. Leaves 12 inches from both sources were about 6° to 8° F warmer than leaves 36 inches from the lights.

Leaf and air temperatures, as measured by the thermocouples under both the 100-watt incandescent and 100-watt fluorescent light sources, were about the same at the 12, 24, and 36-inch distances. However, there was a decreasing temperature gradient as the distance from the light source increased (Figs. 3, 4). At the 2-inch distance from the fluorescent light source, leaf and air temperatures were also about the same, but at 2 inches from the incandescent light the leaves were about 10° to 15° F warmer than the air.

The light intensity data presented in Table 1 help to explain the temperature difference. At 2 inches from the 100-watt incandescent source the light intensity, as measured by a Weston Illumination Meter, was greater than at 2 inches from the 100-watt fluorescent source. At 12, 24, and 36 inches from the light source, the intensity was greater under the 100-watt fluorescent light source than under either the 100-watt or 150-watt incandescent light sources.

The leaf temperatures (Table 2) are closely related to the light intensities measured. When the average air temperature over a 24-hour period (curtains were open from 0800 to 1700 permitting air circulation) was measured, the thermocouple 2 inches from the 100-watt fluorescent light source averaged about 3° F cooler than the one 2 inches from the incandescent light source. At the 12, 24, and 36-inch distances, thermocouples under the fluorescent lights averaged 1° to 2° F warmer than those at the same distances from the incandescent lights. The air was 4° to 6° F cooler under the 40-watt fluorescent than under the 100-watt fluorescent source at all distances measured. Air temperatures under the 150-watt incandescent source averaged from 1° to 3° F warmer than those under the 100-watt incandescent source, over the 24-hour period.

It has been demonstrated (Gelin and Burström, 1; Withrow and Withrow, 6; and Wiggans, 5) that plants grow better, in photoperiodic experiments, when the supplemental light source is furnished from a fluorescent source rather than from an incandescent source. This probably is

Table 1. Light intensities, in foot-candles, at different distances from fluorescent and incandescent lights in light chambers with curtains closed, as measured by a Weston Illumination Meter, Model 756 with quartz filter.

Distance from light	Fluorescent		Incandescent	
	40-watt	100-watt	100-watt	150-watt
2"	530	1500	2100	2900
12"	125	370	270	350
24"	40	150	110	130
36"	20	80	50	55

Table 2. Average air temperature, in degrees F, for a 24-hour period 0800 Jan. 11 to 0800 Jan. 12, for different distances from fluorescent and incandescent lights (24-hour light sources).

Distance from light	Fluorescent		Incandescent	
	40-watt	100-watt	100-watt	150-watt
2"	78.6°	85.2°	88.3°	91.6°
12"	74.6	78.6	77.8	78.5
24"	70.9	75.2	73.1	74.6
36"	67.4	71.7	70.9	72.6

due to the fact that radiation from fluorescent lights is more satisfactory for plant growth than radiation from incandescent lights per wattage of power output involved. In order to make equal intensities of light available to the plant it is necessary to use a higher wattage of incandescent light which gives a greater heating effect (Table 1).

SUMMARY

Leaf and air temperatures were measured in photoperiod chambers by means of thermocouples placed at various distances from the lights. Both incandescent and fluorescent lights were used as light sources. Unshielded thermocouples, which gave a close approximation of "true" air temperature, were used to measure air temperatures.

Leaves exposed to 100-watt fluorescent light sources were slightly warmer at 12, 24, and 35-inch distances from the source than those exposed at similar distances from the 100-watt incandescent light source. However, at the 2-inch distance, leaves exposed to the incandescent light were from 10° to 15° F warmer. Leaf temperatures, except for those very close to the source, seem to depend almost entirely on the intensity of the light, which in turn depends on the wattage of the source and the distance from the source.

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LIFE HISTORY OF THE BLACK BULLHEAD,
AMEIURUS MELAS (RAFINESQUE), OF CLEAR LAKE, IOWA¹

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Bullhead fishing is a favorite sport of many Iowa anglers. Bullheads have been cited as the fish with the most widespread popularity in Iowa (8). The abundance and average size of the bullheads in Clear Lake have changed in recent years and partially as a result of these changes the angling effort and success have been better in some years than in others.

Clear Lake, in Cerro Gordo County, north-central Iowa, is a shallow eutrophic lake of glacial origin. The surface area is 3,643 acres and the drainage area is not much greater than the lake basin. Each summer since 1947, data on the limnology and fish populations of Clear Lake have been collected by biologists of the Iowa Cooperative Fisheries Research Unit. Some additional information was collected in 1941 and 1943. Although a few yellow bullheads, *Ameiurus natalis* (Le Sueur), have been recorded from Clear Lake (1), practically all of the bullheads examined from the lake in recent years have been *Ameiurus melas*.

MATERIALS AND METHODS

The present study of the black bullhead is based upon data collected at Clear Lake by the Cooperative Unit biologists in 1943 and from 1947 through 1954. In some years the bullhead apparently received little attention and only a few measurements are available for these years. In 1951, William Percy and the author made a special effort to collect data on bullheads and these data provide the body of this report.

In analyzing the 1951 data, three topographically distinct areas were recognized and it was found that each of these areas had populations of bullheads which were separate and distinguishable for at least the summer period. The east end of the lake is oval, 2.1 miles wide by 3.8 miles long with a maximum depth of 20 feet. In 1951 emergent vegetation in this section was scattered and only limited beds of submerged vegetation existed. Bottom materials in shallow water areas are predominately sand grading into muck at depths of over seven feet. The east end is almost separated from the west end of the lake by the Lone Tree Point and the peninsula now known as McIntosh Woods State Park. The west end

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of Clear Lake, has a maximum width of 0.7 mile, a maximum length of 1.0 mile and a maximum depth of 7 feet. Both emergent and submergent vegetation line most of the shore of the west end, although the vegetation was not dense in 1951. Ventura Marsh, the third area, was at one time broadly connected to the west end of the lake but a road fill and a state carp trap completely isolate this area at the present time. By mid-July in 1951 most of Ventura Marsh was filled with submerged and emergent vegetation.

All weights, measurements, and examinations of adult bullheads were made while the fish were fresh. Some length measurements were made on young-of-the-year bullheads preserved in 10 percent formalin. Standard length was measured from the tip of the snout to the crease formed by flexing the tail. Total length was measured from the tip of the snout to the end of the caudal fin when the latter was slightly compressed. For convenience in changing from one measurement to another the following conversion factor has been calculated:

$$\text{Standard length} = 0.833 \text{ total length.}$$

This factor is based on 654 bullheads, 8 inches to 12 inches in total length. Within this range of lengths a single conversion factor was found to be sufficiently precise. There was, however, evidence that the tail becomes a smaller proportion of the total length as the fish increase in size. The conversion factors for the different size ranges were as follows:

Standard length	Number of fish	Conversion factor
6.5-7.4	138	0.826
7.5-8.4	318	0.831
8.5-9.4	142	0.838
9.5-10.2	55	0.843

Lewis (7) described alternating dark and light bands on the centra of bullhead vertebra, which were interpreted as annual marks from which the age of the fish could be determined. Portions of the vertebral column were collected in 1950, 1951, and 1952 for studying age and growth. Dorsal spines and opercles were also taken from many of the same fish in 1951 to determine whether these structures might give better clues to age and growth than the vertebra. The sections of the vertebral column, dorsal spines and opercular bones were stored in scale envelopes and allowed to thoroughly dry. When the dried vertebral column was broken apart the vertebral centrum was usually left clean and ready for observation under a low power binocular scope. The opercular bones were cleaned of dried tissue after being dipped in hot water. The markings could be recognized without further treatment or magnification. A thin circular saw (4) was used to cut cross sections of the spines slightly above the base of articulation. The sections were mounted in a drop of xylol and viewed with transmitted light under a standard scale projector. For more permanent mounts the sections were stuck to the slide with a small amount of clear fingernail polish. Xylol can then be added whenever it is desired to observe the sections.

Nearly all adult bullheads collected in 1950 and 1952 were taken in experimental gillnets. In 1951, 1953, and 1954, wire trap and wing nets

Table 1. Mean total lengths in inches of black bullheads taken by various gear during consecutive 10-day periods, beginning June 21, 1951. (Numbers of specimens given in parentheses)

	1	2	3	4	5	6	7	8
Gillnet	8.95 (107)	9.23 (65)	9.72 (113)	10.00 (37)	10.42 (51)	10.97 (50)	10.97 (50)	11.11 (34)
Bagnet		9.23 (23)						
Wing net	8.98 (63)			10.28 (21)				
Wire trap	9.12 (45)		9.38 (56)					

were employed to supplement the gillnet catch. A comparison of the mean lengths of bullheads taken by different methods shows there was no appreciable gear selectivity within the 8-12 inch size range which existed in 1951 (Table 1). There were, however, indications that the relative plumpness of the fish in the various samples was influenced by the method of capture.

In the east end of Clear Lake in 1951 the mean ponderal-index (see later discussion for formula) of 364 bullheads taken in gillnets was 3.30, the ponderal-index for 101 taken in wire traps was 2.82 and the ponderal-index value for 91 captured in hoop nets was 2.90. The differences between the ponderal-index values of fish captured by gillnets, wing nets and wire traps when evaluated by analysis of variance were found to be significant at the one per cent probability level ($F = 32.66$; $n_1 = 2$, $n_2 = 553$). A subdivision of the catch by each type of gear on the basis of area and depth showed that the various gear were sampling from a common population.

The apparent gear selectivity is due in part to the length of time between capture and the recording of measurements. Gillnets were raised at two hour intervals while traps and wing nets were raised at 12 to 24 hour intervals. As a result, bullheads collected from traps and wing nets seldom had food in their stomachs while half of those taken in gillnets contained appreciable amounts of food. In addition, most bullheads taken in gillnets had swallowed large amounts of water. Measurements of stomach contents made in connection with food studies indicated that the difference in fullness of the stomach would cause a 10 gram difference in weight between fish captured in gillnets and those taken in wing nets and wire traps. Since the observed difference in ponderal-index values would be equivalent to a 48 gram difference in weight between a gillnet and a trap caught bullhead of 10 inches in length, the manner in which the bullheads were handled only partly accounts for the observed difference in plumpness.

In the statistical comparison of length-weight data it has been necessary to rely primarily on samples collected with gillnets. There is, however, no basis for believing the length-weight relation of bullheads taken in gillnets better represents the actual condition in the population than the length-weight relation based on bullheads taken with different gear.

Growth and Age Determination

Schools of young of the year bullheads were abundant around the shores of Clear Lake in 1943, 1945, 1946, 1947, 1951, 1952, 1953, and 1954. Samples of these fish were measured at weekly or ten-day intervals to determine the growth during the summer (Table 2). The growth of young bullheads was apparently slower in 1951 than in the other years. The summer of 1951 was particularly cool with mean June, July, and August temperatures of 62.8°, 70.0°, and 67.0°F, respectively. These temperatures were 4.1°, 3.0°, and 3.2° below normal at the Mason City weather station (U. S. Weather Bureau, Climatological Data).

While it was relatively simple to determine the age group of the young-of-the-year bullheads by their size, the age of older bullheads often cannot be so readily ascertained. In 1950, vertebral samples were collected from 96 bullheads seined or netted in scattered areas of Clear Lake. Of these, 12 with an average total length of 9.9 inches had six or seven evenly spaced year marks on the centra similar to those described by Lewis (7). The age of this group could not be determined with any degree of certainty. No bullheads with similar centrum markings were found in 1951 or 1952 collections. The remaining 84, averaging 7.4 inches, had four year marks on the centra. The first three marks were close together, with the fourth broadly separated from the third. This spacing of the first four year marks was characteristic of all adult bullheads collected in 1951 and 1952. On the basis of the vertebral markings it is believed the 84 bullheads collected in 1950 and all of the adult bullheads netted in 1951 and 1952 were survivors of the 1946 year class.

A fifth year mark was present on the centra of adult bullheads examined in 1951 and a sixth year mark on the centra of bullheads collected in the summer of 1952. Young of the year bullheads seined in October 1951 did not have any markings on the centra which could be interpreted as year marks. Yearlings taken in the summer of 1952 had either a single or double dark ring on the centrum. The paired rings were so closely associated that there was no danger of interpreting them as separate year marks.

The addition of a mark on the centrum each year and their consistent arrangement within a year class suggests the centrum markings are valid indices of age. A disturbing development was the appearance of a well defined dark ring on the centrum of many of the bullheads in July 1951. Since it was the second mark to appear in 1951 it must be considered a false year mark although no satisfactory character could be found to separate this structure from the markings considered to be true year marks. The possibility of additional false rings cannot be denied, but records of spawning success in previous years indicate these bullheads probably cannot be more than one year older or younger.

The Lake Survey Unit of the Iowa State Conservation Commission found young of the year bullheads to be abundant in Clear Lake in 1945, 1946, and 1947 but absent in 1948 and 1949. The vertebral markings of all individuals are so similar that it must be assumed that the entire 1951 sample was composed of only one year class. Yearling bullheads were seen in the spring of 1947, but not in 1948. It is probable that the first winter is a critical period in a bullhead's life. A heavy mortality of young bull-

Table 2. Total lengths in inches of black bullheads in Clear Lake, Iowa, during their first summer of growth

	Ten day periods beginning						
	July 1	July 11	July 21	July 31	August 10	August 20	August 30
1943							
Mean	1.11	-	1.48	2.19	-	-	-
Number	81	-	86	61	-	-	-
Range	.7-1.2	-	.9-2.0	1.5-2.6	-	-	-
1951							
Mean	.74	1.06	1.19	1.30	1.43	1.80	1.78
Number	66	85	555	912	156	98	140
Range	.6-.9	.8-1.3	.8-1.9	.7-2.6	.9-2.4	1.2-2.9	1.3-2.8
1952							
Mean	1.07	1.47	1.82	2.11	2.60	3.00	-
Number	50	70	142	63	57	127	-
Range	.8-1.2	.9-1.7	1.0-2.3	1.3-2.6	1.9-3.4	2.0-3.9	-
1953							
Mean	1.23	.8	1.47	2.04	1.78	2.06	-
Number	83	1	2910	49	49	11	-
Range	1.0-1.5	-	1.2-1.9	1.3-2.4	1.2-2.4	1.7-2.6	-
1954							
Mean	-	1.33	1.50	1.47	1.76	1.96	2.14
Number	-	2050	3618	110	3700	1461	22
Range	-	0.9-1.5	0.9-1.8	0.8-1.9	1.2-2.2	1.4-2.4	1.7-2.6

heads of the abundant 1951 year class was observed in the winter of 1951-52 and in the spring of 1952 as the ice went out.

Opercular bones and dorsal spines were removed only from bullheads netted in 1951. Two zones of alternate translucent and opaque bone tissue extended across the posterior area of the opercular bones examined. The structure of the bands was similar to the markings described by LeGren (6) on perch opercula and English (3) on carp opercula. Both authors were able to show that the opercular markings corresponded to scale annuli on the same fish. On the bullhead opercula the zones representing the first three years of life which would be expected from observations of the vertebral markings were not visible. Evidently the thickening of the anterior portion of the opercula had obscured these marks.

Magnified images of spine sections showed alternate narrow bands of translucent bone tissue separated by broader opaque bands. The translucent areas corresponded closely in position and number to the dark rings on the vertebral centra. This similarity between spine markings and vertebral markings suggests that they may be equally valid indicators of age but the spine markings were often poorly defined and the spines required more preparation before observations could be made than was required for vertebral centra.

Since the 1946 year class was the only group of large bullheads, it has been relatively simple to follow their growth through 1954 even without referring to vertebral markings (Table 3). Growth was apparently quite

Year of collection and age group	March to June 21	Ten day periods beginning									
		June 21	July 1	July 11	July 21	July 31	Aug. 10	Aug. 20	Aug. 30	Aug. 30	
<u>1947-I</u>											
Mean	2.46	-	-	-	-	-	-	-	-	-	
Number	147										
Range	1.8-3.8										
<u>1948-II</u>											
Mean	-	-	6.50	6.97	6.77	-	7.05	-	-	-	
Number			3	11	3		14				
Range			6.4-6.6	6.1-8.0	6.3-7.3		6.5-7.2				
<u>1950-IV</u>											
Mean	-	7.13	-	7.85	7.86	7.85	8.00	8.07	-	-	
Number		21		9	27	165	85	34			
Range		6.2-8.9		7.2-9.3	7.3-9.5	6.8-9.7	6.7-9.7	7.0-8.6			
<u>1951-V</u>											
East End											
Mean	-	9.00	9.24	9.60	10.06	10.43	10.91	11.07	11.10		
Number		217	115	172	62	62	34	62	36		
Range		8.1-10.4	8.2-10.3	8.3-10.7	9.0-11.2	9.2-11.7	9.6-11.9	9.4-12.0	9.9-11.8		
West End											
Mean	-	8.70	9.15	-	-	-	10.53	-	11.26		
Number		15	16				9		30		
Range		8.0-9.6	8.4-9.8				9.7-11.4		10.2-12.0		
Ventura											
Mean	-	-	-	9.11	9.31	9.36	9.81	-	10.22		
Number				77	16	150	52		10		
Range				8.2-10.2	8.8-10.7	8.3-10.5	8.8-12.2		9.3-10.8		
<u>1952-VI</u>											
Mean	11.34	12.01	11.53	11.67	10.85	11.47	11.83	11.96	11.53		
Number	19	7	51	176	56	36	30	32	6		
Range	10.3-12.2	11.4-12.6	10.4-12.3	10.3-12.7	9.1-12.2	9.9-12.7	9.8-12.9	11.2-13.3	10.3-12.3		
<u>1953-VII</u>											
Mean	11.95	11.78	12.4	11.90	11.98	12.13	-	10.8	-		
Number	32	6	1	25	25	11		2			
Range	10.2-12.2	11.0-12.8		10.4-13.6	11.0-13.0	11.0-12.6		10.7-10.9			
<u>1954-VIII</u>											
Mean	12.22	12.65	12.03	12.08	11.57	12.1	-	-	-		
Number	82	2	3	5	3	1	-	-	-		
Range	11.0-13.5	12.2-13.1	11.9-12.3	11.3-13.2	10.9-12.4	-					

slow from 1948 through 1950. The weekly increase in total length of the 1946 year class between June 21 and August 30 averaged 0.04 inch in 1950 and 0.24 inch in 1951. Samples taken over a similar period in 1952 show an unusual fluctuation in mean length with little indication of any growth. The mean length for each 10 day period in 1952 and 1953 was frequently based on fish from a single gillnet set, suggesting that the observed fluctuation in mean length is the result of sampling schools or isolated populations within the east end. This hypothesis was supported by an analysis of variance of mean lengths of bullheads caught in individual gillnet sets made in various areas of the east end. Differences in the mean lengths were significant at the 1 per cent level. A similar fluctuation in mean lengths of bullheads from different gillnet sets was observed in 1951, however, the effect of sampling subpopulations was obscured in the 1951 data shown in Table 3 by combining several gillnet sets for each period mean. In 1950 nearly all bullheads were taken at a single station, which may account for the absence of similar fluctuations in the 1950 data.

Bullheads grew at a slightly more rapid rate in the west section of Clear Lake than in the east section during the summer of 1951 (weekly increment, 0.25 inches and 0.24 inches total length respectively). During the same period the weekly increment for the Ventura Marsh population was 0.09 inches total length. The relatively slow growth in Ventura Marsh may have been caused by a Clinostomum epizootic which centered in this area. In August nearly 100 per cent of the bullheads collected from Ventura Marsh were heavily infected with the metacercariae stage of Clinostomum complanatum, while less than 1 per cent were infected in the east and west end.

The average sizes in 1952, 1953, and 1954 indicate that there has been comparatively little growth of this year class in their 7th to 9th years of life. By the late summer of 1954 comparatively few of this once predominant year class were surviving in the lake. In Lost Island Lake, Iowa, Rose and Moen (10) were able to follow the 1941 year class of bullheads to their tenth year. The age group IX bullheads in Lost Island Lake average 10.4 inches total length, considerably smaller than the Clear Lake bullheads. The Lost Island bullheads were considered a stunted overcrowded population until large numbers were harvested in 1946 to 1948.

As already mentioned, vertebra of 12 bullheads collected in 1950 indicated that they probably belonged to the 1944 or 1943 year class. In 1948, measurements were taken on 18 bullheads obviously of one or more earlier year classes. They were 8.0 to 11.7 inches long and averaged 10.68 inches, total length.

In 1952, specimens of the 1951 year class began to appear in the catch and it has been possible to follow the growth of this and the 1952 year class through 1954 because the size ranges are fairly distinct (Table 4). At age group II, the average size of the bullheads in the 1951 and 1952 year classes appears to be about the same as that of the 1946 year class.

Length-Weight Relationship

Differences in the length-weight relationships or relative plumpness of bullheads captured by gillnets, wire traps, and hoop nets in 1951 have already been pointed out. In studying length-weight relationships, only

Table 4. Total lengths in inches of the 1951-53 year classes of black bullheads in Clear Lake, Iowa, 1952-1954

Year Class Year of Col- lection and Age Group	Ten day periods beginning									
	April	May	June 11	June 21	July 1	July 11	July 21	July 31	Aug. 10	Aug. 20
1951 Year Class										
1952-I	-	-	-	-	-	-	5.11		5.18	
Mean							9		10	
Number							4.8-5.4		4.6-5.9	
Range										
1953-II	-	-	5.96	5.88	6.23	6.59	6.67	7.28	7.06	7.55
Mean			57	95	114	115	49	24	11	4
Number			4.8-7.9	4.8-7.7	4.8-8.0	4.8-8.9	5.0-7.9	6.2-8.6	6.3-7.9	7.3-7.8
Range										
1954-III	8.30	9.06	-	8.18	8.45	8.36	8.44	8.43	8.39	8.57
Mean	21	16	-	12	16	85	34	354	40	85
Number	7.0-10.5	7.8-10.5	-	7.8-9.0	7.6-9.0	7.6-9.2	7.5-9.5	7.5-9.4	7.7-9.4	7.6-10.1
Range										
1952 Year Class										
1953-I	-	-	-	-	-	-	-	-	-	5.22
Mean										7
Number										4.9-6.1
Range										
1954-II	-	-	-	-	-	7.03	6.90	6.48	6.45	6.80
Mean						10	4	5	4	30
Number						6.3-7.5	6.5-7.2	6.1-7.1	6.0-7.0	6.2-7.4
Range										
1953 Year Class										
1954-I	2.40	-	-	-	5.20	4.67	5.0	4.97	-	5.14
Mean	34	-	-	-	3	9	5	17	-	167
Number	1.9-2.7	-	-	-	4.8-5.9	4.4-5.1	4.5-5.6	4.5-5.4	-	4.2-6.0
Range										

the gillnet samples, therefore, were used. The ponderal index, representing the relative plumpness or condition of the individual fish, was calculated from the expression:

$$K = \frac{10^5 \cdot W}{L^3}$$

where W = weight in grams and L = standard length in millimeters. Where statistical comparisons were desirable and large samples were available, length-weight regressions were calculated using the formula:

$$\text{Log } W = a + n \text{ Log } L$$

where W = weight in grams and L = standard length in millimeters.

The mean ponderal index values for bullheads in different gillnet sets indicated that sampling was not from a homogeneous population. This was in accordance with conclusions reached on the basis of the variation in mean length for bullheads in different gillnet sets. An example of the variation in K factors is provided by a series of gillnet samples collected in the east section of Clear Lake during a ten day period in 1951:

No. of fish	Mean K	Standard deviation
5	2.68	0.049
30	2.97	0.054
13	3.20	0.214
8	3.24	0.087
18	3.26	0.157
55	3.50	0.046

A similar and statistically significant variation in the mean ponderal index values for different gillnet sets was evident in 1952. However, sampling was less intensive in 1952 and it is not possible to determine whether the observed fluctuation in K factors have resulted from sampling different subpopulations or reflect seasonal changes in plumpness.

The length-weight relationships for black bullheads collected in the east section of Clear Lake in various years were determined as:

$$1950 \text{ Log } W = -4.25806 + 2.86030 \text{ Log } L$$

$$1951 \text{ Log } W = -4.04929 + 2.80060 \text{ Log } L$$

$$1952 \text{ Log } W = -2.84768 + 2.28541 \text{ Log } L$$

A test of the homogeneity of the regressions (11) for three years showed there was little chance the slopes of the regression lines were the same ($F = 35.33$, $n_1 = 1$, $n_2 = 711$). Although the adjusted mean weights differed ($F = 188.70$, $n_1 = 2$, $n_2 = 713$) the relative plumpness of the bullheads in 1950, 1951, and 1952 can best be judged from the ponderal index values for the three years (Table 5). The adjusted mean weights of the 1951 and 1952 east end samples are the same but the slopes differed and the 1952 fish were lighter for their length than the 1951 fish.

Bullheads collected from the three sections of Clear Lake in 1951, could be separated by differences in length-weight relations. The equations for the three sections were as follows:

$$\text{Ventura Marsh Male Log } W = -2.59148 + 2.15644 \text{ Log } L$$

$$\text{Female Log } W = -2.18788 + 1.97035 \text{ Log } L$$

$$\text{West end Log } W = -3.67574 + 2.61964 \text{ Log } L$$

$$\text{East end Log } W = -4.04928 + 2.80060 \text{ Log } L$$

Table 5. Ponderal index values for Clear Lake bullheads, 1946 year class
(Number of specimens given in parentheses)
Ten day periods beginning with June 21

Year	Area	Period										Average	Adjusted mean weight at	
		1	2	3	4	5	6	7	8			grams	215.4 mm S.L.	or 10.2" T.L.
1950	East end	2.53 (6)		2.86 (8)	2.71 (24)	2.63 (15)	2.73 (13)					2.70 (66)	260	9.2
1951	East end	3.38 (113)	3.13 (84)	3.26 (111)	3.09 (46)	3.18 (58)	3.22 (34)	3.02 (69)	2.87 (44)			3.18 (559)	305	10.7
	West end	2.87 (16)	2.95 (18)				3.00 (10)		2.57 (26)			2.86 (56)	273	9.6
	Ventura			3.12 (74)	2.81 (15)	2.84 (125)		2.78 (52)	2.64 (10)			2.90 (276)		
	Males			3.28 (13)	2.59 (6)	2.85 (9)		2.80 (7)	2.67 (6)			2.91 (41)	275	9.7
	Females			3.12 (18)	2.70 (6)	2.92 (13)		2.74 (12)	2.60 (4)			2.90 (53)	256	9.0
1952	East end	2.97 (26)	2.79 (51)	2.87 (40)	2.80 (48)	2.96 (34)	2.86 (35)	2.94 (23)				2.87 (257)	305	10.7

The Ventura Marsh bullheads were the only group in which sexual differences in condition may have existed; males averaging 12.7 grams heavier than females when the weights were adjusted by analysis of covariance to a mean length of 195.2 mm ($F = 4.56$, $n_1 = 1$, $n_2 = 76$). Further tests comparing the male bullheads in the three sections indicated significant differences in the regressions ($F = 9.95$, $n_1 = 1$, $n_2 = 274$) and in the adjusted mean weights ($F = 27.13$, $n_1 = 2$, $n_2 = 276$). Similar results were obtained when the equations for the female bullheads from the three sections were compared (regression $F = 38.91$, $n_1 = 1$, $n_2 = 244$; adjusted mean weight $F = 51.76$, $n_1 = 2$, $n_2 = 246$).

The nonhomogeneity of the regressions for the three sections of Clear Lake was affected by a seasonal decline in the plumpness of the Ventura Marsh bullheads which was evident from a decline in the ponderal index values (Table 5). The east and west end regressions are essentially parallel ($F = 2.31$, $n_1 = 1$, $n_2 = 446$) with the east end bullheads averaging 35.1 grams heavier than west end bullheads at a mean length of 209.2 mm ($F = 22.15$, $n_1 = 1$, $n_2 = 447$).

Food and Parasites

The analysis of the stomach contents of 327 bullheads taken between June 21 and September 15, 1951 provides an indication of their food habits during this period of rapid growth. Each stomach was examined individually and the per cent of the total volume which each item contributed was estimated. The average volume and the occurrence of each item is shown in Table 6. An analysis of the bottom fauna collected during the same period is provided by Wm. Pearcy (9).

The predominance of chironomids as a food item, almost entirely Tendipes tentans, probably reflects the abundance of this species in the bottom samples. A certain amount of selectivity was exhibited by individual bullheads, which is illustrated by a two-hour gillnet catch of 12 bullheads from the west end. Eight stomachs contained only chironomids and organic detritus. The organic detritus corresponds to the partially decomposed bottom deposits and may represent the chironomid cases. Three stomachs contained filamentous algae with a few Hyalella, which were particularly abundant in filamentous algae mats. A single bullhead had been feeding exclusively on entomostraca. Not in all cases was the selectivity so marked, but in general a single type of food predominated in the stomach contents.

The stomach contents of over 100 young-of-the-year bullheads, 0.6 to 2.1 inches in total length, were examined during the summer of 1951 (Table 7). Young bullheads less than 0.9 inches long fed on entomostraca to the exclusion of other food. Beyond this size, chironomid larvae and Hyalella were taken in gradually increasing quantity, although entomostraca remained an important part of the diet throughout the first summer. Similar feeding habits were found for young-of-the-year black bullheads in Buckeye Lake, Ohio (5).

Of the adult bullheads collected in 1951, 399 were examined for parasites. Five internal parasites were detected and their occurrence recorded (Table 8). The only external parasites noted were leeches which were occasionally found attached near the base of the fins on a few bullheads.

Table 6. Food of the adult black bullhead in various sections of Clear Lake expressed as frequency of occurrence and as percentages of total volume of food organisms, Summer 1951*

Area	West end of Clear Lake		Ventura Marsh		East end of Clear Lake	
Number of stomachs taken	71		55		201	
Number of stomachs containing food	46		21		111	
Percent of stomachs containing food	64.8		38.2		55.2	
Average volume of stomachs containing food (cc.)	3.0		1.4		4.5	
	Occur- rence	Volume	Occur- rence	Volume	Occur- rence	Volume
Insects						
Diptera (Chironomidae)	34	76.3	13	49.6	110	81.9
Trichoptera	6	12.8	5	40.0	4	22.5
Ephemeroptera	2	12.5	6	33.3	1	10.0
Odonata	1	15.0	2	20.0	-	-
Coleoptera (adult)	-	-	-	-	2	17.5
Crustaceans						
Hyalella	7	13.6	15	24.7	12	9.2
Entomostraca	5	53.0	7	47.9	5	33.4
Mollusca						
Gastropoda	5	6.6	3	6.7	6	17.5
Plant material						
Filamentous algae	17	41.8	2	15.0	8	13.1
Higher aquatic plants	5	19.0	-	-	-	-
Seeds of aquatic plants	4	26.2	-	-	-	-
Organic detritus	31	9.2	9	25.0	100	12.2
Leeches	-	-	3	28.3	1	20.0
Fish						
Northern common shiner	1	100.0	-	-	-	-
Yellow perch	1	100.0	-	-	-	-
Unidentified	1	90.0	-	-	3	80.0

*The percentages of volume refer only to the stomachs which contained that item.

Table 7. Food of the 1951 young of the year black bullheads in Clear Lake, Iowa, expressed as frequency of occurrence and as percentages of total volume of food organisms.*

Total length (mm.)	16 to 25		26 to 35		36 to 45		46 to 55	
Number of stomachs	54		26		17		26	
	Occur- rence	Vol- ume	Occur- rence	Vol- ume	Occur- rence	Vol- ume	Occur- rence	Vol- ume
Insects								
Diptera	5	56.0	12	48.3	8	24.0	17	42.9
Chironomidae								
Trichoptera					1	5.0	1	5.0
Agraylea sp.					1	15.0	2	20.0
Ephemeroptera							2	20.0
Coleoptera (adult)								
Crustaceans								
Hyalella sp.	8	46.1	25	58.4	13	65.0	21	41.8
Entomostraca	53	96.1	17	39.4	13	48.1	17	60.3
Acarina								
Hydrachnidae	1	5.0	1	5.0				
Leeches							1	15.0

*The percentages of volume refer only to the stomachs which contained that item.

Two species of tapeworms, Corallobothrium fimbriatum and C. giganteum, were found in the upper intestine, ranging in abundance from 1 to over 100 in a single fish. Even infestations of over 20 tapeworms had no apparent effect on the condition of bullheads as measured by K factors. The acanthalla stage of Neoechinorhynchus cylindratus was found encysted in the liver, causing local tissue damage, but the infestations were always light. Another parasite appearing in the liver was the larval tapeworm, Proteocephalus ambloplitis. Occasionally P. ambloplitis was observed in the ovaries, where it caused a thickening and hardening of the ovarian tissue and a destruction of immature eggs (Table 8).

Table 8. Frequency of occurrence of important parasites in Clear Lake bullheads expressed as percentages of total number examined (1951)

	East and west end	Ventura Marsh
Number of bullheads examined	316	83
<u>Proteocephalus ambloplites</u>	18	13
<u>Corallobothrium</u> *	31	29
<u>Clinostomum complanatum</u>	1	31
<u>Neoechinorhynchus cylindratus</u>	23	11

*Corallobothrium fimbriatum and C. giganteum combined.

Clinostomum complanatum, the yellow grub, was found in the metacercarial stage encysted in the general body musculature. The C. epizootic was limited to Ventura Marsh where infestations exceeding 500 cysts per bullhead were recorded. The distortion of tissue caused by cysts lying close to the dermis was externally evident and appeared in nearly all specimens netted in late August and in September. The possible relation of Clinostomum to retarded growth and poor condition has been discussed in a previous section.

A limited number of young-of-the-year bullheads were examined for parasites. A single, unidentified, immature cestode was found in the intestinal tract of one specimen. A severe infestation of C. complanatum was found in Ventura Marsh, but appeared in less than 3 per cent of the young-of-the-year from other sections of the lake. Many dead and dying young-of-the-year bullheads less than 1.0 inch in length were recovered from Ventura Marsh by seining during June and July. Characteristically these had one or more distinct cysts upon the head in addition to others on the trunk. These individuals were emaciated, and commonly found weakly swimming along the shore. In these small bullheads the individual cyst was sufficiently large to cause severe local distortion of the musculature which possibly interfered with feeding and visibly interfered with swimming.

Reproduction and Survival

The great differences in the abundance of bullheads from various year classes direct attention to reproduction and to survival of the young fish.

The ovaries of all female bullheads observed in 1951 were mature, containing large ova representing the 1951 spawn with numerous minute eggs lining the ovarian wall. The first spent female was taken June 26 and the last ripe female August 6. The peak of the spawning period probably occurred early in July. Young-of-the-year were first seined July 7 and became increasingly abundant as the season progressed. In 1947, Robert Cleary recorded in his field notes that bullheads were still spawning on June 29.

Fecundity was estimated by the volumetric method. The minute ova adhering to the ovarian wall were excluded in this determination. The ovaries of 19 females, 8 to 8.9 inches long, contained an average of 3,283 eggs, with a standard deviation of 152. The ovaries of 24 females, 9 to 9.9 inches long, contained an average of 3,845 eggs, with a standard deviation of 222.

Bullhead spawning beds were not located, but the distribution of young-of-the-year suggests that aquatic vegetation is associated with spawning success. Soft stem bullrush and submergent vegetation border approximately one-half the shore line of the east end. Numerous schools of bullheads were found within this border of vegetation after the middle of July but during the same period no bullhead schools were observed along non-vegetated shore line. Seining along the shore supported these observations. In late August a few schools were located along the north shore where vegetation was lacking but migration from other areas may account for their appearance.

Young-of-the-year bullheads were very numerous in 1945, 1946, and 1947 when aquatic vegetation was at a maximum in Clear Lake. Vegetation was very sparse in 1948 to 1950 and no young bullheads were seen in 1948 and 1949 and only a few small schools were seen in 1950. The very successful reproduction in 1951 occurred when vegetation was recovering. Vegetation has been moderately abundant in 1952 to 1954 and bullhead reproduction has been successful.

Behavior of Young-of-the-Year

The strong schooling tendency of the young black bullheads makes observation of their habits relatively simple. Adults were observed tending schools along the shore where the water was greater than two feet in depth. On 8 out of 13 occasions two or more adults accompanied a single school; on the other occasions only one adult was observed. Samples taken from four schools tended by adults indicated that the total length of the young ranged from 0.6 inches to 1.0 inches. Apparently the adults desert the young shortly after the latter size is reached and the schools move into shallow water near shore. In mid-July samples from schools within 4 feet of shore ranged from 0.8 inches to 1.4 inches in total length. As the summer progressed the lower limit remained at 0.8 inches while the upper limit increased to 2.4 inches, indicating that schools along the shore were subject to recruitment from late hatches. After mid-August

the lower limit of the total lengths gradually increased to 1.3 inches by mid-September.

The movements of young-of-the-year bullheads in Ventura Marsh deviated from the pattern described for the main part of the lake. After the schools were deserted by the adults, the schools congregated in the shallow water for a brief period but later roamed freely throughout the lake. Perhaps this habit may be explained by the heavy growth of submergent vegetation which fills most of the Ventura Marsh.

Young-of-the-year bullheads were observed in 1945, 1946, 1947, and 1950 but of these only the 1946 year class appeared to survive. The cause of this mass mortality of year classes remains unknown, but observations on the 1951 hatch perhaps give some clues. This year class suffered little mortality until late fall when dead young-of-the-year were readily seined along the shore. The following spring, numerous dead, 2-3 inch bullheads lined the shore indicating that the late fall and winter were a critical period for these fish. No evidence of disease or parasites was detected in these fish. The heavy mortality of young bullheads in Ventura Marsh from Clinostomum took place in July.

There was no evidence in the summer of 1951 that predation restricted the density of the bullhead population. The stomachs of many walleyes (Stizostedion vitreum), yellow perch (Perca flavescens), young northern pike (Esox lucius), and yellow bass (Morone interrupta) were examined without discovering any bullhead remains. There may be other times when these species may exert a significant predatory pressure on young bullheads, but none was noted in 1951.

In past years, many dead adult bullheads have been seen along the shores of Clear Lake in May and June. It is believed that these mortalities may be associated with spawning activities. Most of the dead bullheads found in June 1951 bore wounds or abrasions which were frequently infected with fungus.

Table 9. Mean catch of bullheads per 24-hour period with 125-foot experimental gill nets near hatchery at Clear Lake, Iowa*

Year	1947	1948	1949	1950	1951	1952
Catch per day	4.8	1.4	0.4	13.4	9.5	16.1
Hours netted	240.5	1084.5	543.0	496.0	895.0	674.0

*From Carlander (2).

Some indication of the relative abundance of bullheads in Clear Lake from the catch per day in the gillnets is shown in Table 9. The substantial increase in the catch in 1950 was probably the result of the dominant 1946 year class reaching catchable size. The angling success over the same period seems to have also been associated with the growth and gradual disappearance of the 1946 class, although a few data are available to substantiate the general observations. In 1953 and 1954, the anglers

began to catch the 1951 and 1952 year class bullheads and these smaller bullheads comprised most of the 1954 catch.

SUMMARY

Data on black bullheads were collected at Clear Lake by the Iowa Co-operative Fisheries Research Unit in 1943 and 1947 to 1954, but principal emphasis was placed upon this species in 1951. Young-of-the-year bullheads were abundant around shore in 1943, 1945, 1946, 1947, 1951, 1952, 1953, and 1954. No young bullheads were seen in 1948 and 1949 and only a few in 1950. Possibly the scarcity of aquatic vegetation in the lake in 1948 to 1950 affected reproduction and survival.

Markings on the vertebral centra collected in 1950, 1951, and 1952 indicated that all the adult bullheads at that time belonged to the 1946 year class, except for a few older fish collected in 1950. Sections of the dorsal spine showed similar markings, but thickening of the central portions of the opercula prevented the use of the latter structure for age determination. The 1946 year class showed rapid growth in 1951 but slow growth from 1948 through 1950 and 1952 through 1954.

In 1951, bullheads of Ventura Marsh, of the east end, and of the west end of the lake differed in growth and in length-weight relationships. The Ventura Marsh bullheads decreased in condition throughout the summer, grew slowly, and were heavily infested with Clinostomum complanatum.

The 1951, 1952, and 1953 year classes began to support the angling in 1953, whereas the 1946 year class alone had supported the fishery for about 3 years.

Food of the adult bullheads was predominately chironomid larvae in 1951. Small young-of-the-year bullheads fed exclusively upon entomostrea, but as their size increased, insect larvae became increasingly important in their diet.

Of the five species of internal worm parasites identified from Clear Lake bullheads, only Clinostomum complanatum appeared to have a significant effect on growth or survival.

Ovaries of 41 female bullheads each contained 3,000 to 4,000 eggs. Late fall and winter appeared to be the critical period in survival of the young bullheads of the 1951 year class. Predation had little effect, at least during the summer of 1951.

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